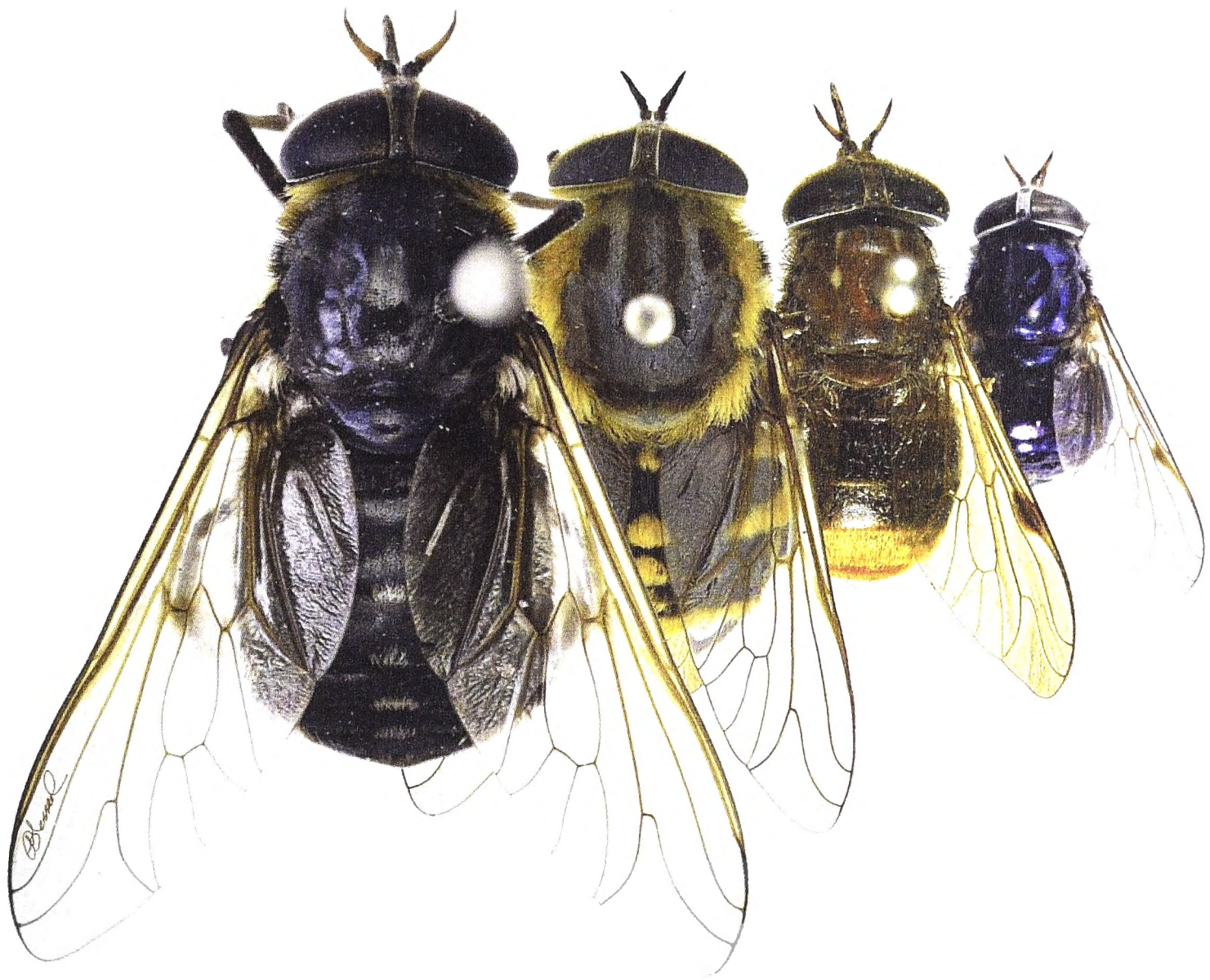
The taxonomy, systematics and biogeography of the austral horse fly tribe Scionini (Diptera: Tabanidae)

Bryan David Lessard



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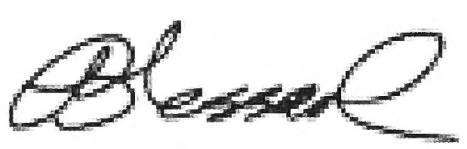
A thesis submitted for the degree of Doctor of Philosophy of The Australian National University

Declaration

I, Bryan David Lessard, declare that this thesis, submitted to the degree of Doctor of Philosophy of The Australian National University, is my own original work unless otherwise referenced or acknowledged. Contributions by others are specified accordingly in each chapter of the thesis. This document has not been submitted for consideration at any other academic institution.



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Preface

This thesis is formatted as a series of publications either submitted or published in peer-reviewed journals. Each journal article represents a single thesis chapter and contains respective methodologies. Due to the structure of the thesis there may be some inevitable repetition among chapters, the General Introduction, General Material and Methods and General Conclusion. Each chapter is provided with a title page detailing the publication information and author contributions. A combined Bibliography is provided at the end of the thesis including references for all chapters. Chapters One to Six refer to the previous taxonomic rankings of the subgenera of *Scaptia* before the formal taxonomic revision is presented in Chapters Seven and Eight. All taxonomy presented in this thesis is only officially recognised upon publication.

Abstract

The Tabanidae are a large cosmopolitan family of medically and ecologically important Diptera. Adults of both sexes are important pollinators, and the females are known to mechanically transmit multiple disease agents while blood-feeding, affecting humans and animals. The tribe Scionini of the subfamily Pangoniinae consists of stoutly built and hairy-eyed flies predominantly austral in distribution, occurring in Australia, New Guinea, New Zealand and South America. The Scionini are divided into six recognised genera; *Caenopangonia* Kröber, 1930, *Fidena* Walker, 1850, *Goniops* Aldrich, 1892, *Pityocera* Giglio-Tos, 1896, *Scione* Walker, 1850, and the widest distributed genus *Scaptia* Walker, 1850. *Scaptia* is further divided into seven subgenera; *Lepmia* Fairchild, 1969, *Pseudomelpia* Enderlein, 1922, *Myioscaptia* Mackerras, 1955, *Palimmecomyia* Taylor, 1917, *Plinthina* Walker, 1850, *Scaptia* Walker, 1850, and *Pseudoscione* Lutz, 1918.

The taxonomy of the Scionini has not been revised in over 50 years. Consequently, new material has accumulated in museums corresponding to 18 new species of *Scaptia* (*Plinthina*) (5 **spp.n.**), *Scaptia* (*Pseudoscione*) (7 **spp.n.**), *Scaptia* (*Scaptia*) (1 **sp.n.**), *Scaptia* (*Myioscaptia*) (2 **spp.n.**), and the novel genus *Anzomyia* Lessard, **gen.n.** (3 **spp.n.**), all of which have been described and illustrated herein.

Molecular data was employed to provide the first quantitative phylogenetic hypothesis for the Scionini, including the systematic placement of all the tribes in the Pangoniinae. An alignment of six molecular markers, including mitochondrial (COI and COII), ribosomal (28S) and nuclear (AATS, CAD regions 1, 3 and 4) genes, 5757 bp in total, was analysed for 176 taxa using Bayesian and maximum likelihood approaches. Results indicated the Scionini are strongly monophyletic, excluding *Caenopangonia* and *Goniops,* which were subsequently removed from the Scionini and reassigned to the Pangoniinae tribes Mycteromyiini and Goniopsinini, Lessard **tribe.n.**, respectively. The South American genera *Fidena, Pityocera* and *Scione* were strongly monophyletic, corresponding to current morphology-based classification schemes. Interestingly, *Scaptia* recovered as broadly paraphyletic, which was corrected by formally raising several subgenera to genus level (*Lepmia*, *Myioscaptia*, *Palimmecomyia*, *Plinthina*, *Pseudomelpia* and *Pseudoscione*), resurrecting previously synonymised genera (*Apocampta* Schiner, 1867, *Copidapha* Enderlein, 1922, *Parosca* Enderlein, 1922, *Osca*

Walker, 1850, and *Triclista* Enderlein, 1922) and establishing a novel genus from New Zealand (*Aotearomyia* Lessard, **gen.n.**). These molecular results were combined with morphological evidence to revise the taxonomy of the entire Scionini, including the redescription of all genera and subgenera, in addition to the development of a novel diagnostic key to all seventeen recognised genera.

Divergence time estimates based on the molecular data and the fossil record placed global biogeographic radiations of the Pangoniinae in a temporal context. Results indicated that the Scionini are a typical Gondwanan group and are most likely Australian in origin. Furthermore, the diversification and current biogeography of the tribe appears to be influenced by the ancient fragmentation of Gondwana, involving a complex process of both vicariance and long distance dispersal. Future studies will benefit from more extensive sampling of the South American genera, in particular *Fidena, Pityocera* and *Scione*, which require further taxonomic revision and updating of the diagnostic keys to species.

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List of Abbreviations

A	Anal vein (wing morphology)
AATS	Alanyl-tRNA synthetase
ABRS	Australian Biological Resources Study
ACT	Australian Capital Territory
AIC	Akaike Information Criterion
AM	Australian Museum, Sydney, Australia
ANIC	Australian National Insect Collection, CSIRO Ecosystem Sciences, Canberra, Australia
AU	Australia
BEAST	Bayesian Evolutionary Analysis Sampling Trees
BS	Bootstrap support value
bp	Base pair
BYU	Brigham Young University, Utah, USA
CAD	Carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase
COI	Cytochrome Oxidase Subunit One
COII	Cytochrome Oxidase Subunit Two
CP	Codon position
CSIRO	Commonwealth Science and Industrial Research Organisation, Ecosystem Sciences, Canberra, Australia
Cu	Cubital vein (wing morphology)
DNA	Deoxyribose nucleic acid
ERM-LUNZ	Entomology Research Museum, Lincoln University, Canterbury, New Zealand
GDCB	Greg Daniels Private Collection, Brisbane, Queensland, Australia
Gen.n.	Genus novum
GTR + I + G	General time-reversible + invariant + gamma model
hLRTs	Hierarchical likelihood ratio test
M	Medial cell or vein (wing morphology)
min	Minute
ML	Maximum likelihood
mm	Millimeter
MNZ	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand

List of Abbreviations

mtDNA	Mitochondrial DNA
MY	Million years
NCSU	North Carolina State University, Raleigh, North Carolina, USA
NMH	The Natural History Museum, London, United Kingdom
NP	National Park
NSF	National Science Foundation, USA
NSW	New South Wales, Australia
NT	Northern Territory, Australia
nuDNA	Nuclear DNA
NZ	New Zealand
PEET	NSF Partnerships Enhancing Expertise in Taxonomy
PP	Posterior probability
Qld	Queensland, Australia
QDPI	Queensland Department of Primary Industries, Indooroopilly, Australia
QM	Queensland Museum, Brisbane, Australia
UQIC	University of Queensland Insect Collection, Brisbane, Australia
USP	University of São Paulo, Ribeirão Preto, Brazil
R	Radial cell or vein (wing morphology)
SA	South Australia (Chapters Three to Six); South America (Chapters One and Seven)
SAM	South Australian Museum, Adelaide, Australia
Sc	Subcosta vein (wing morphology)
SD	Standard deviation
Sec	Second
SI	Smithsonian Institute, Suitland, Maryland, USA
Sp.n.	Species novum
Spp.n.	Multiple species novum
Stat.n.	Status novum
Tas	Tasmania, Australia
Trans.n.	Translocation novum
Tribe.n.	Tribe novum
USA	United States of America
Vic	Victoria, Australia
WA	Western Australia
WAM	Western Australian Museum, Perth, Australia

28S	Ribosomal 28S gene
µL	Microliter
°C	Degree Celsius
*	Type species (Chapters Five and Seven); specimens physically examined by authors (Chapter Eight)
†	Type species (Chapters Six and Eight); revised genera of *Scaptia* Walker, 1850 (Chapter Seven)

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Chapter One

1. General Introduction

The Diptera are one of the most diverse insect orders and largest radiations of terrestrial eukaryotic organisms (Wiegmann *et al.* 2011). The order comprises 10-15% of the known animal species and approximately 150,200 described species (Yeates *et al.* 2003, 2007; Wiegmann *et al.* 2011). This species rich group has been divided into over 150 families, 22-32 superfamilies, 8-10 infraorders and 2 suborders (Yeates and Wiegmann 1999; Yeates *et al.* 2007). The suborder Brachycera comprises the "higher Diptera" with shortened antennae, and is further divided into four monophyletic infraorders: the Xylophagomorpha, Stratiomyomorpha, Muscomorpha and Tabanomorpha (Wiegmann *et al.* 2003, 2011; Yeates and Wiegmann 1999), with the latter including the horse flies (Diptera: Tabanidae).

1.1 The Tabanidae

The Tabanidae, commonly referred to as horse, deer or march flies, are a cosmopolitan family of the Diptera with over 4400 described species (Evenhuis *et al.* 2009; Pape and Thompson 2012). Both males and females are vital pollinators of many plants, feeding on the nectar of Australian *Eucalyptus, Grevillea* and *Melaleuca,* along with other myrtaceous plants such as *Leptospermum* in Australia and New Zealand (Johnson and Morita 2006; Mackerras 1957, 1960; Morita 2008; Tillyard 1926). The family also exhibits sexually dimorphic feeding habits, as adult females are known blood-feeders and can mechanically transmit several disease-causing microbes, spreading anaplasmosis (Scoles *et al.* 2008) and bovine leukaemia virus in cattle, equine infectious anaemia in horses (Foil *et al.* 1984, 1988), trypanosomiases and infections of the filarial nematode *Pelecitus roemeri* in Macropods such as the kangaroo and wallaby (Spratt 1972a, 1972b, 1974a, 1974b, 1975; Reid *et al.* 2001), in addition to loiasis, tularaemia and anthrax in humans (Foil 1989; Krinsky 1976). Therefore, the Tabanidae have considerable medical and ecological importance.

1.2 Classification of the Tabanidae

The classification of the Tabanidae is fairly stable as a result of the extensive work of Mackerras (1954, 1955) who provided the current scheme based on the external and genitalic characters of adults which is still used today. This scheme encompasses four subfamilies (Figure 1), with further division into one to four tribes: Chrysopsinae (Bouvieromyiini, Chrysopini and Rhinomyzini), Pangoniinae (Mycteromyiini [added by Coscarón and Philip, 1979], Pangoniini, Philolichini and Scionini), Scepsidinae, and the largest of the subfamilies Tabaninae (Diachlorini, Haematopotini and Tabanini).

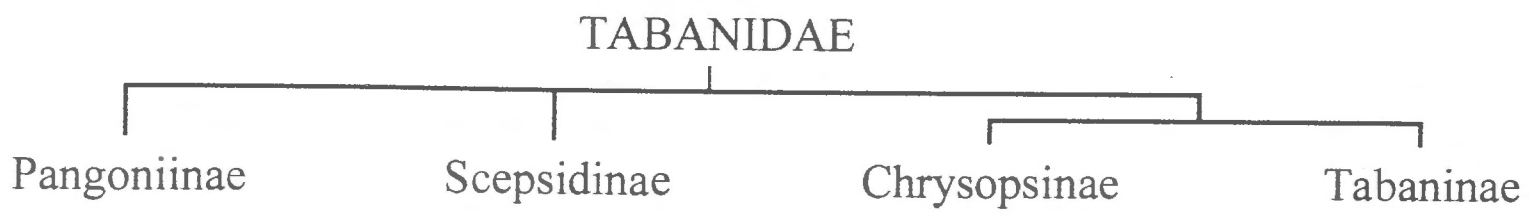


Figure 1: Mackerras' (1954, 1955) classification scheme for the subfamilies of the Tabanidae.

The subfamily Pangoniinae has a near global distribution and are formed of long proboscis flies with relatively long and slender legs, appearing well adapted to grasp flowers (Mackerras 1955). Currently the Pangoniinae consists of four tribes: the Mycteromyiini (Neotropical in distribution), Pangoniini (Australasian, Nearctic, Neotropical and Palaeartic), Philolichini (Afrotropical, Australasian and Oriental) and the Scionini (Australasian, Nearctic and Neotropical) (Coscarón and Philip 1979; Mackerras 1954, 1955; Morita 2008).

1.3 The tribe Scionini Enderlein, 1922

The Scionini are mostly stout, bearded and hairy-eyed flies. The tribe is currently divided into six genera, of which some are further divided into subgenera (Figure 2), including *Caenopangonia* Kröber, 1930, *Fidena* Walker, 1850, *Goniops* Aldrich, 1892, *Pityocera* Giglio-Tos, 1896, *Scaptia* Walker, 1850, and *Scione* Walker, 1850. The tribe is predominantly austral in distribution, occurring in Australia, New Guinea, New Zealand and South America, with the exception of the monotypic Nearctic genus *Goniops* (Coscarón and Wilkerson 1985; Coscarón and Gonzalez 2001; Coscarón and Iide 2003; Mackerras 1957, 1960, 1961, 1964; Oldroyd 1947; Wilkerson and Coscarón 1984). *Goniops* and *Caenopangonia* notably differ from the remainder of Scionini by the presence of the bare eyes and extremely widened frons in the females. Knowledge regarding the larval stages of the tribe is known only for *Goniops* and *Scaptia* (Coscarón and González 1989; English 1955; Mackerras 1955, 1957, 1960), as the extreme limitation of material available for examination has hindered the development of a formal diagnosis for these stages.

1.3.1 The genus Goniops *Aldrich, 1892*

The Nearctic genus *Goniops* is monotypic and represented by a single medium-sized (12-14 mm), concolorous golden-brown species (Figure 2). The genus is diagnosed by the presence of bare eyes and wings prominently stained radially with brown (Brennan 1935; Mackerras 1955; Stone 1930). *Goniops* is restricted to the eastern United States of America and is the only member of the Scionini to occur in the Northern Hemisphere (Mackerras 1955).

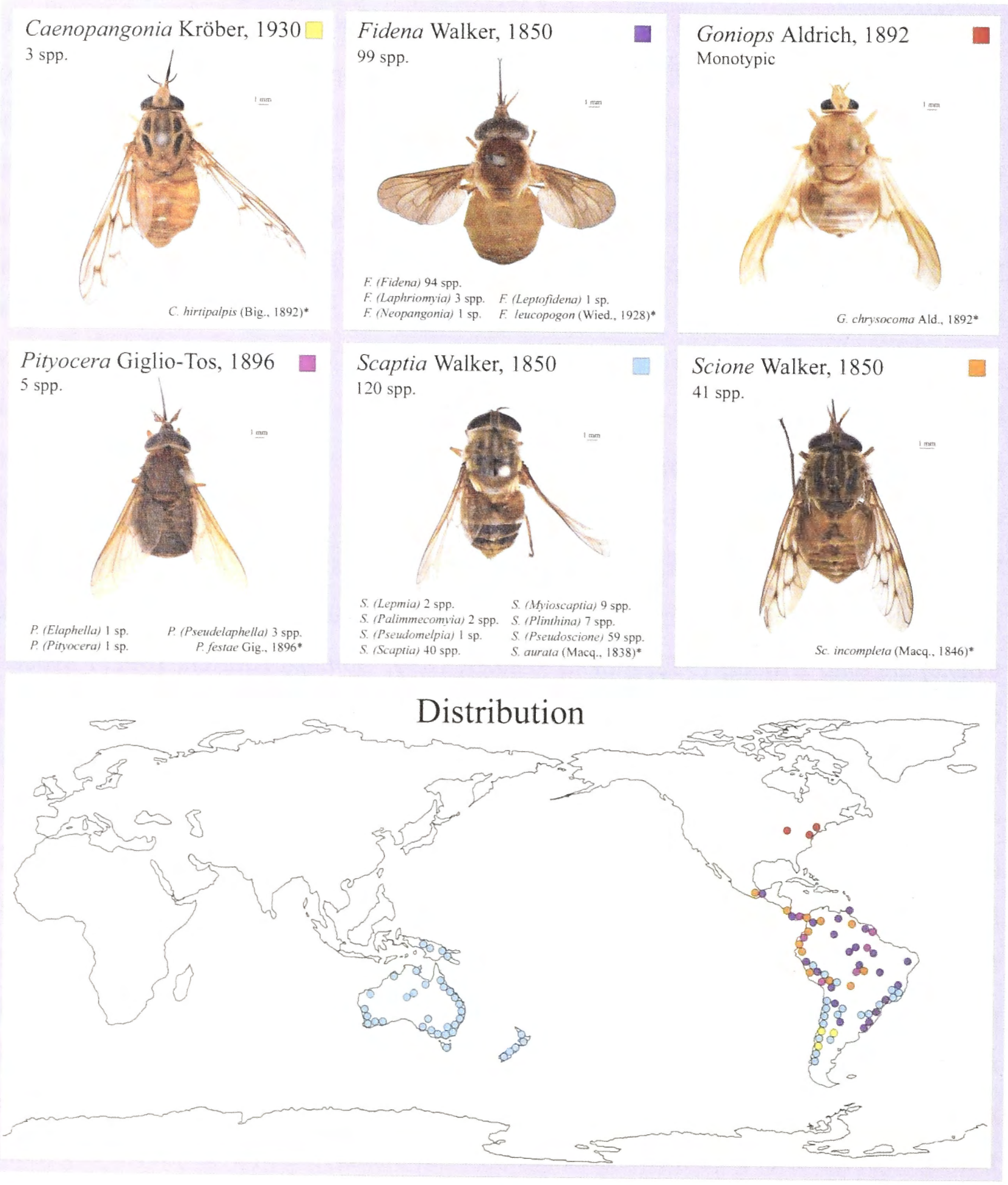


Figure 2: The distribution of the austral horse fly tribe Scionini, including genera, subgenera and species richness. All type species are illustrated, with the exception of *Caenopangonia brevirostris* (Philippi, 1865).

1.3.2 The genus Caenopangonia *Kröber, 1930*

The South American genus *Caenopangonia* comprises small to medium-sized species (length 9-14 mm), yellowish-brown in colour (Figure 2), and is the only member of the Scionini to possess dichoptic eyes in both sexes (Coscarón and Philip 1979; Kröber 1930b). The genus contains three described species from Chile and Argentina (Coscarón and Philip 1979; Kröber 1930b). Mackerras (1955, p. 483) previously reduced

Caenopangonia as a synonym of *Mycteromyia* Philippi, 1865, however, Coscarón and Philip (1979) resurrected *Caenopangonia* and "questionably retained" the genus within the Scionini (Coscarón and Philip 1979, p. 427). Based on the morphological differences in the dichoptic eyes of the male and extremely wide and densely haired frons of the females, *Caenopanngonia* appears to be more congruent with the Mycteromyiini than the Scionini. Therefore, the taxonomic placement of *Caenopangonia* may warrant reconsideration.

1.3.3 The genus Fidena *Walker, 1850*

The genus *Fidena* includes medium to large (11-22 mm), stout species with a distinctly produced snout-like face and an extremely long, slender proboscis (Figure 2; Coscarón and Papavero 2009; Mackerras 1955). *Fidena* is widespread throughout South America, with a smaller radiation into Central America (Coscarón and Papavero 2009; Mackerras 1955). Currently, the genus contains 99 described species and is further divided into four subgenera, including *Fidena* (*Fidena*) Walker, 1850 (94 spp.), *Fidena* (*Laphriomyia*) Lutz, 1911 (3 spp.), *Fidena* (*Leptofidena*) Kröber, 1930 (monotypic), and *Fidena* (*Neopangonia*) Lutz, 1909 (monotypic).

1.3.4 The genus Pityocera *Giglio-Tos, 1896*

Pityocera is formed of small to medium-sized (length 8-14 mm), concolorous brown species, most similar to *Fidena* sharing a projecting face and long proboscis equal to or greater than the length of the body (Figure 2). It is distinguished from other Scionini by the antennal flagellum with obvious structural projections or prominent tufts of hairs on one or more flagellomeres (Fairchild 1942, 1969; Mackerras 1955; Coscarón and Papavero 2009). The genus is predominantly distributed in South America, with a smaller expansion in Central America. *Pityocera* currently contains five described species and is further divided into three subgenera; *Pityocera* (*Pityocera*) Giglio-Tos, 1896 (monotypic), *Pityocera* (*Elaphella*) Bezzi, 1913 (monotypic), and *Pityocera* (*Pseudelaphella*) Kröber, 1930 (3 spp.).

1.3.5 The genus Scione *Walker, 1850*

Scione is formed of rather small to moderately-sized (length 9-16 mm), slender and uniformly mottled species, diagnosed by the projecting face, proboscis with unexpanded labella, and strongly patterned thorax, abdomen and spotted wings (Figure 2; Fairchild 1942; Mackerras 1955; Coscarón and Papavero 2009). The genus comprises 41 described species from Central and South America, ranging from Mexico, Guatemala and Panama to Colombia, Venezuela, Ecuador, Brazil, Peru, Bolivia and Argentina (Fairchild 1942; Mackerras 1955). Based on the morphological similarities of the scutal vittae and overall appearance, it may be closely related to the subgenus *Scaptia* (*Pseudoscione*) Lutz, 1918.

1.3.6 The genus Scaptia *Walker, 1850*

The most widespread genus *Scaptia* comprises mostly solidly built species and is the most species-rich genus of the Scionini, with over 120 described species. The genus is exclusively austral in distribution, occurring in Australia, New Guinea, New Zealand and South America (Coscarón and Wilkerson 1985; Coscarón and González 2001; Coscarón and Iide 2003; Mackerras 1957, 1960, 1961, 1964; Oldroyd 1947; Wilkerson and Coscarón 1984). *Scaptia* is further divided into seven subgenera, including *Lepmia* Fairchild 1969, *Pseudomelpia* Enderlein 1922, *Myioscaptia* Mackerras 1955, *Palimmecomyia* Taylor 1917, *Plinthina* Walker 1850, *Scaptia* Walker 1850, and *Pseudoscione* Lutz, 1918.

The subgenus *Scaptia* (*Scaptia*) includes short, thick-legged species (Figure 2), possessing parallel frons, large pointed and sabre-like palpi, and a short and thick proboscis with large well-developed labella (Coscarón and Wilkerson 1985; Mackerras 1955, 1960). It is the second most widely distributed subgenus of *Scaptia*, occurring in Australia and South America and contains 40 described species (Coscarón and Wilkerson 1985; Mackerras 1955, 1960; Wilkerson 1984). Several former genera have been reduced to synonymies of *Scaptia* by Ferguson (1924, 1926), based on shared morphology, including *Apocampta* Schiner, 1867 (from Australia), *Triclista* Enderlein, 1922 (Australia) and *Osca* Walker, 1850 (South America), which is adopted by most authors (Coscarón and Papavero 2009; Coscarón and Wilkerson 1985; Fairchild 1969; Mackerras 1955, 1960; Wilkerson 1984).

The three subgenera *Scaptia* (*Myioscaptia*), *Scaptia* (*Palimmecomyia*) and *Scaptia* (*Plinthina*) are endemic to Australia (Mackerras 1960). *Scaptia* (*Myioscaptia*) is formed of nine described species that are small (8-11 mm) and rotund, usually bright metallic green to dull semi-metallic black, with rounded leaf-like palpi (Mackerras 1955, 1960). In contrast, the subgenus *Scaptia* (*Plinthina*) contains only seven medium-sized species (9-14 mm), with strong scutal vittae, distinct marbling of the wings, and short thick and broad flattened palpi (Mackerras 1960). The subgenus *Scaptia* (*Palimmecomyia*) is represented by only two described species that are long (13-17 mm), narrow to elongated, parallel-sided and wasp-like in appearance (Mackerras 1955, 1960; Taylor 1917).

The subgenera *Scaptia* (*Lepmia*) and *Scaptia* (*Pseudomelpia*) are both endemic to South America (Coscarón and González 2001; Coscarón and Iide 2003). The Brazilian subgenus *Scaptia* (*Lepmia*) is formed of only two moderately-sized species (length 11-15.5 mm), diagnosed by the broad and densely haired, large bulbous abdomen and the thick proboscis with reduced labella (Fairchild 1969; Coscarón and Iide 2003). In contrast, the monotypic Chilean subgenus *Scaptia* (*Pseudomelpia*) is small (length 7-9 mm), dark and hairy, and diagnosed by the extremely short and thick proboscis, short swollen club-like palpi, and basal fusion of the antennal flagellomeres (Coscarón and Papavero 2009; Coscarón and González 2001; Kröber 1930b; Mackerras 1955).

The most widespread subgenus *Scaptia* (*Pseudoscione*) contains 59 described species from Australia, South America, New Guinea and New Zealand, and is the only representative of the Scionini in the latter two islands (Mackerras 1957, 1960, 1961, 1964; Oldroyd 1947; Wilkerson and Coscarón 1984). Species are plump, medium-sized to rather large (range 9-16 mm), and diagnosed by the long and slender proboscis with small labella and relatively long slender legs (Mackerras 1955, 1960). Two former genera, *Copidapha* Enderlein, 1922 (Australia) and *Parosca* Enderlein, 1922 (Chile), were reduced to synonymies of *Scaptia* (*Pseudoscione*) by Ferguson (1926) and Mackerras (1955), respectively, based on shared morphology, and is adopted by most authors (Coscarón and Papavero 2009; Fairchild 1956, 1966; Mackerras 1960; Daniels 1989; Wilkerson and Coscarón 1984).

Mackerras (1960) described one curious species, *Scaptia* (*Pseudoscione*) *anomala* Mackerras, 1960, from Australia and suggested that it may represent a novel subgenus of *Scaptia*. Although unnamed at the time, Mackerras (1955) referred to the species as being

most similar to *Scaptia* (*Pseudoscione*), based on shared similarities of the antennal flagellomeres and genitalia, but also sharing the short fleshy proboscis and large, hairy antennal scape that is most similar to *Scaptia* (*Pseudomelpia*). The species was also identified as an intermediate species of *Scaptia* (*Scaptia*) and *Scaptia* (*Pseudoscione*), and was provisionally placed within *Scaptia* (*Pseudoscione*) so it would not escape recognition: "*S. anomala* is exceptional, in combing the short proboscis and long palpi of [the subgenus] *Scaptia* with the diverging frons and general appearance of [the subgenus] *Pseudoscione*… a case could be made for establishing [a new subgenus] for *Scaptia,* [represented by] *S. anomala*, and that may prove to be a proper course when more is known about it" (Mackerras 1960, p. 33).

1.4 Challenges of traditional taxonomy

The taxonomy of the Scionini has been historically challenging, since many of the genera are often weakly diagnosed by the combination of relatively few morphological characters that are not necessarily useful or informative when applied to other groups. Identifications based on the genitalia are often compromised because large structural differences in the genitalia do not correspond to differences in external morphology, and often cannot aid in species identification (Mackerras 1955, 1960). Mackerras (1960) stated that there is an "absence of supporting differences in the genitalia" (p. 32) and that "the male genitalia have given no assistance in discriminating between species" (p. 36) of Australian Scionini. Preservation can also impact on common diagnostic characters, such as the augmentation of proboscis length during death (Wilkerson and Coscarón 1984) that can impede subgeneric diagnoses, or colour fading in specimens that can affect species-level identification (Mackerras 1960; Mackerras *et al.* 2008).

Mackerras (1955, p. 455) lamented "the situation is further complicated by the large number of species in the family, repeated evolution, paucity of structural characters, and the fact that segregates are quite distinct in one region but merge together in another, so that workers in different regions would naturally have different opinions about their validity". The taxonomy of the South American genera is particularly fragmented and has been considered to be in a "chaotic condition" (Fairchild 1956, p. 9). Moreover, many international workers have made several disjoint taxonomic changes for several genera of the Scionini that are published in a myriad of languages, including English, German

and Spanish (Lutz *et al.* 1918; Kröber 1930a; Enderlein 1922, 1925). The original taxonomy for some genera is often inadequate and incomplete, with Enderlein (1922) and Lutz *et al.* (1918) presenting several original genera (*Pseudomelpia* and *Pseudoscione,* now recognised as subgenera of *Scaptia*, and the synonymised genera *Copidapha* Enderlein, 1922, *Parosca* Enderlein, 1922, and *Triclista* Enderlein, 1922) in either a taxonomic key or checklist to species, without a formal taxonomic description or any systematic context. Consequently many genera may have been wrongly synonymised in the past due to a poor understanding of their taxonomy and systematic relationships.

1.5 Previous molecular studies on the Tabanidae

Recent workers have found strong support for the monophyly for the Tabanidae, based on both morphological (Mackerras 1954; Yeates 2002) and molecular evidence (Morita 2008; Wiegmann *et al.* 2000, 2003, 2011). Molecular data was recently proven successful in reconstructing phylogenetic histories for the Tabanidae, as Wiegmann *et al.* (2000) was the first to demonstrate the well-supported monophyly of the Tabanidae using the ribosomal gene 28S (Figure 3). In this previous study, each subfamily was recovered as monophyletic, including two species of the Chrysopsinae, four species of the Tabaninae, and two species of the Pangoniinae, each belonging to the tribes Mycteromyiini and Pangoniini (Wiegmann *et al.* 2000).

Wiegmann *et al.* 2003 also reinforced the monophyly of the Tabanidae using 28S data, however, included only two specimens corresponding to the subfamilies Chrysopsinae and Tabaninae. More recently, the phylogenomic approach of Wiegmann *et al.* (2011) showed that the Tabaninae subfamily was strongly monophyletic using a dataset of complete mitochondrial genomes and 12 nuclear and ribosomal genes, including mitochondrial Cytochrome Oxidase (CO), ribosomal 28S and the nuclear protein-coding genes carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD) and alanyl tRNA synthase (AATS), despite the family being represented by a single specimen from each of the genera *Tabanus* and *Haematopota*.

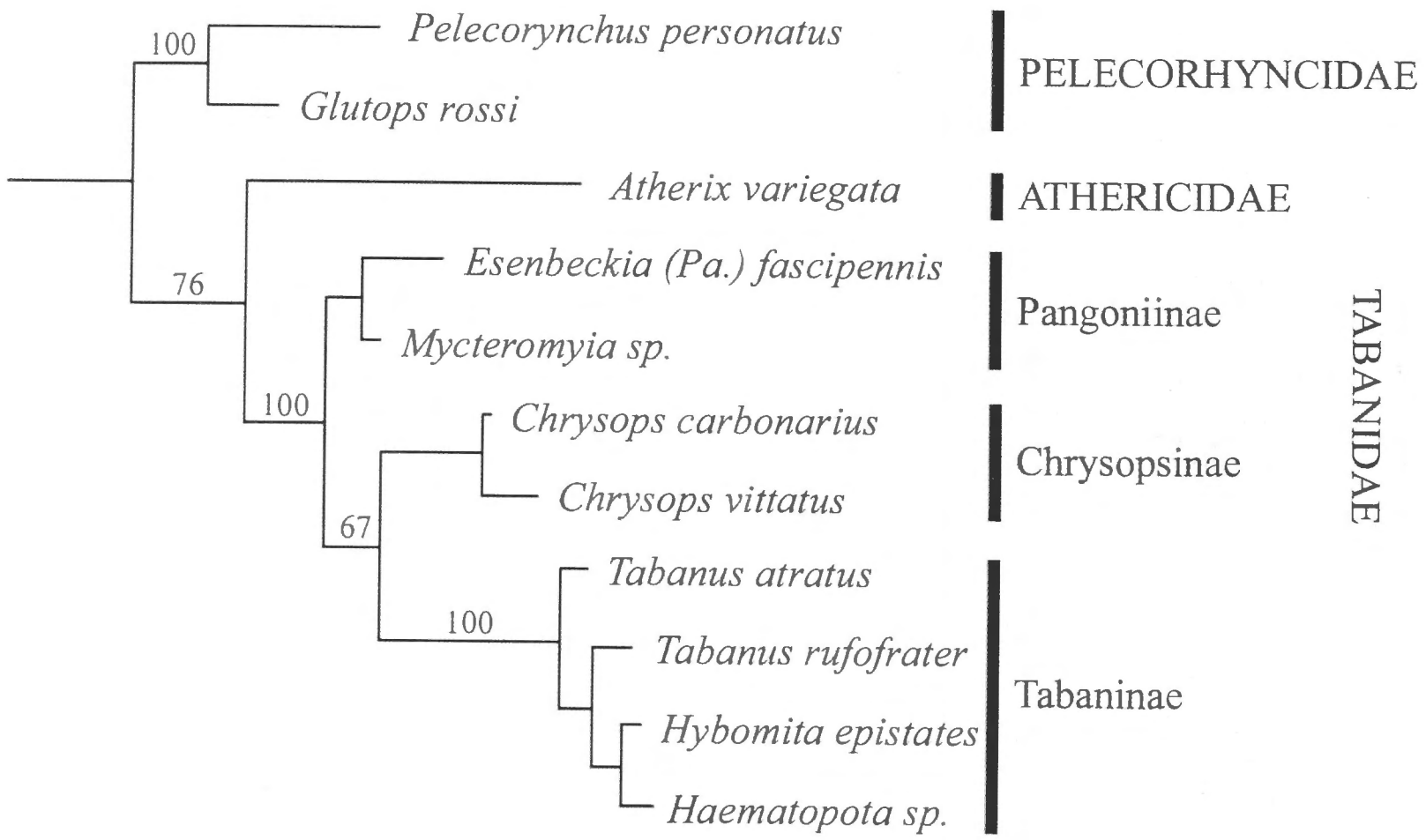


Figure 3: Phylogenetic relationships of the Tabanomorpha presented by Wiegmann *et al.* (2000: modified from figure 3, p. 1036). Note the monophyly of the Tabanidae and its subfamilies based on maximum likelihood analysis of ribosomal 28S data (bootstrap support >50%; 100 replicates).

The molecular study of Morita (2008) was the first to explore the phylogenetic relationships of the Tabanidae below the subfamily level. Using the mitochondrial gene Cytochrome Oxidase Subunit One (COI) and the carbamoyl-phosphate synthetase domain of the nuclear gene CAD, Morita (2008) demonstrated strong support for the monophyly of each subfamily (Figure 4), in addition to the individual monophyly of two of the four Pangoniinae tribes, the Pangoniini and Philolichini. The traditional morphological classification schemes for the tribes were also supported by the molecular analysis of Morita (2008). Currently, studies on the phylogenetic relationships of the Tabanidae remain extremely limited and do not include any members of the tribe Scionini.

1.6 Divergence time estimation

Divergence time estimation combines genetic data with the fossil record to date divergences among lineages in a time-calibrated phylogeny (Crisp *et al.* 2011; Wiegmann *et al.* 2003). Recent workers have successfully applied divergence time estimation to investigate the diversification events of the holometabolous insects

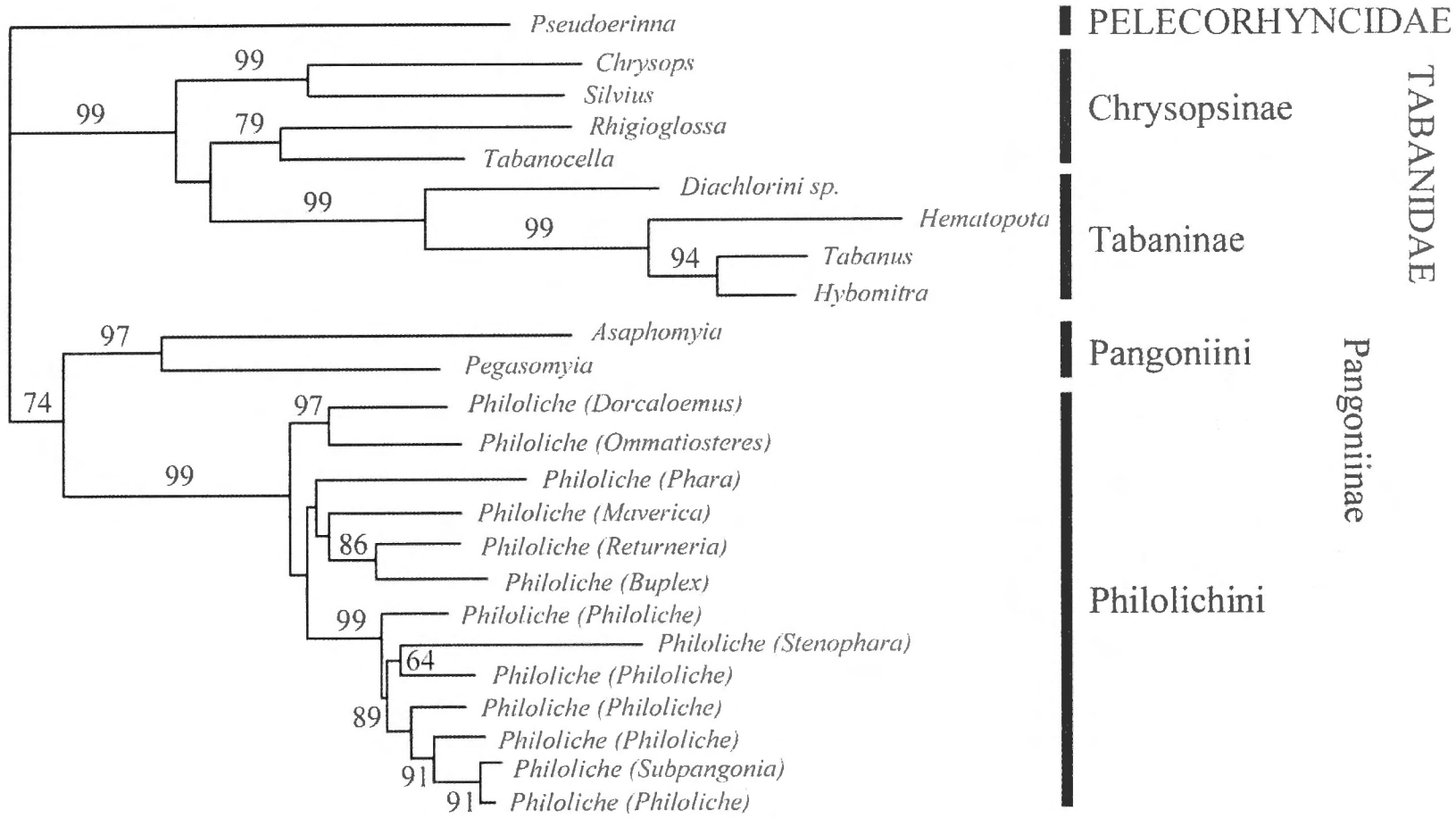


Figure 4: Phylogenetic relationships of the Tabanidae presented by Morita (2008: modified from figure 5, p. 320). Note the monophyly of the Tabanidae, including the tribes of the Pangoniinae subfamily based on maximum likelihood analysis of CAD and COI genes (bootstrap support > 50%; 1000 replicates).

(Wiegmann *et al.* 2009), the Neuropterida (Winterton *et al.* 2010) and the Diptera (Bertone *et al.* 2008; Wiegmann *et al.* 2003, 2011), including the fly families Acroceridae (Winterton *et al.* 2007), Agromyzidae (Winkler *et al.* 2009) and Stratiomyidae (Brammer and von Dohlen 2007). Bertone *et al.* (2008) placed the earliest diversification of the Diptera approximately 267 MY ago in the late Permian using multiple gene markers, including CAD and 28S. The results of Bertone *et al.* (2008) was somewhat in accordance with the estimate for the earliest diversification of the Diptera placed at 245 MY, based on fossil data alone (Grimaldi and Engel 2005).

Wiegmann *et al.* (2003) was the first to include the Tabanidae in a larger study assessing the temporal divergences of the Brachycera. This previous study revealed the Tabanidae diverged from the Pelecorhynchidae approximately 120-115 MY ago in the Cretaceous, with the Chrysopsinae and Tabaninae subfamilies diverging approximately 57 MY ago in the early Paleogene. This study, however, included only two specimens corresponding to the subfamilies Chrysopsinae and Tabaninae and used a single fragment of the 28S gene. Therefore, previous studies on the temporal diversification of the Tabanidae are extremely limited and divergence time estimation may provide novel insights into the global diversification patterns of the family.

Table 1: The fossil Tabanidae, including age, collection substrate and taxonomic placement (Martins-Neto and Santos, 1994; Mostovski *et al.* 2003; Ren 1998; Zhang 2012).

Fossil name	Age (MY)	Formation, country	Position	Reference
Laiyangitabanus formosus	145-140	Laiyang Formation, China	Tabanidae	Zhang 2012
Eotabanoid lordi	144-140	Durlston Formation, England	Tabanidae	Mostovski *et al.* 2003
Eopangonius pletus	127-121	Yixian Formation, China	Tabanidae	Ren 1998
Cratotabanus stenomyomorphus	121-99	Crato Formation, Brazil	Tabanidae	Martins-Neto and Santos, 1994
Cratotabanus sp.	121-99	Crato Formation, Brazil	Tabanidae	Martins-Neto and Santos, 1994

1.7 The fossil Tabanidae

Fortunately there are several reasonably well-preserved fossils of Tabanidae that can be used to calibrate divergence time estimates for the family. These comprise five fossilised species spaning four genera (Table 1) that are considered to be the most reliable, including *Cratotabanus stenomyomorphus* Martins-Neto and Santos, 1994 and *Cratotabanus* sp. Martins-Neto, 2003 (both 121–99 MY; Crato Formation, Brazil; Grimaldi *et al.*, 2011; Martins-Neto, 2003; Martins-Neto and Santos, 1994), *Eopangonius pletus* Ren, 1998 (127–121 MY; Yixian Formation, China; Ren, 1998), *Eotabanoid lordi* Mostovski, Jarzembowski and Coram, 2003 (144–140 MY; Upper Berriasian Durlston Formation, England; Mostovski *et al.*, 2003) and *Laiyangitabanus formosus* Zhang, 2012 (145–140 MY; Late Tithonian, Upper Jurassic to Early Berriasian, Lower Cretaceous; Laiyang Formation, China; Zhang, 2012). Unfortunately, many of these fossils cannot be accurately assigned to a particular subfamily due to the failed preservation of key diagnostic features, such as the hind tibial spurs, antennal flagellum and ocelli (Mostovski *et al.*, 2003; Zhang, 2012).

The fossils originally described by Ren (1998) in the subfamily Pangoniinae have either been criticised as belonging to that subfamily or have been subsequently removed altogether from the Tabanidae. Based on the preserved wing morphology, Grimaldi *et al.* (2011) identified *Palaepangonius eupterus* Ren, 1998 (127–121 MY; Yixian Formation, China; Ren, 1998) as being inconsistent with the Tabanidae, specifically regarding the short inverted R_{2+3}, the open cell *Cu* with veins A_1 and CuA_2 independently meeting at the wing margin, and the extremely long veins R_4 and R_5 that are double the length of extant

Tabanidae. Based on these differences, the genus was eventually transferred to the Athericidae and synonymised under the genus *Athericites* Mostovski, Jarzembowski and Coram, 2003 (Zhang 2012). Similarly, *E. pletus* is no longer recognised as a member of the Pangoniinae, as it cannot be assigned to any of the subfamilies due to the failed preservation of the diagnostic hind tibial spurs and antennal flagellum (Zhang, 2012). *Baissomyia redita* Mostovski, Jarzembowski and Coram, 2003 (137–127 MY; Lower Cretaceous; Zaza Formation, Russia; Mostovski *et al.*, 2003), which was provisionally described within the Tabanidae, also cannot be confidently placed within the family due to the poor preservation of the wings and is currently recognised as a stem group of the Tabanomorpha (Mostovski *et al.*, 2003).

The compression fossils *E. lordi* and *La. formosus* which span two continents (China and the UK) are currently considered to be the oldest and most reliable fossils of the Tabanidae, based on the almost complete preservation of the wings (Mostovski *et al.*, 2003; Zhang, 2012). Refering to *E. lordi*, Mostovski *et al.* (2003, p. 165) stated that "the general shape of the wing, the much thickened basal costal vein, the long and nearly straight R_{2+3} [vein], and the broad R_{4+5} fork unequivocally place the genus in the Tabanidae". Therefore, the known ages of the two independent fossils will be valuable for estimating the divergence times of the Tabanidae.

1.8 Gondwana and the biogeography of the Scionini

Gondwana was once the southern division of the ancient supercontinent Pangaea, separating from Laurasia approximately 180-160 MY ago in the Jurassic (Figure 5; Sanmartín and Ronquist 2004). The great southern continent began to fragment 165-150 MY ago, with Africa becoming completely separated from the remaining landmass at 110-95 MY in the mid-Cretaceous (Sanmartín and Ronquist 2004). Zealandia, the ancient landform that would eventually give rise to New Zealand, was the first to break away from the remainder of Gondwana 82-70 MY ago in the late Cretaceous, followed by the complete separation of Australia, Antarctica and South America from one another between 40-28 MY ago in the Paleogene (Crisp *et al.* 2011; Sanmartín and Ronquist 2004).

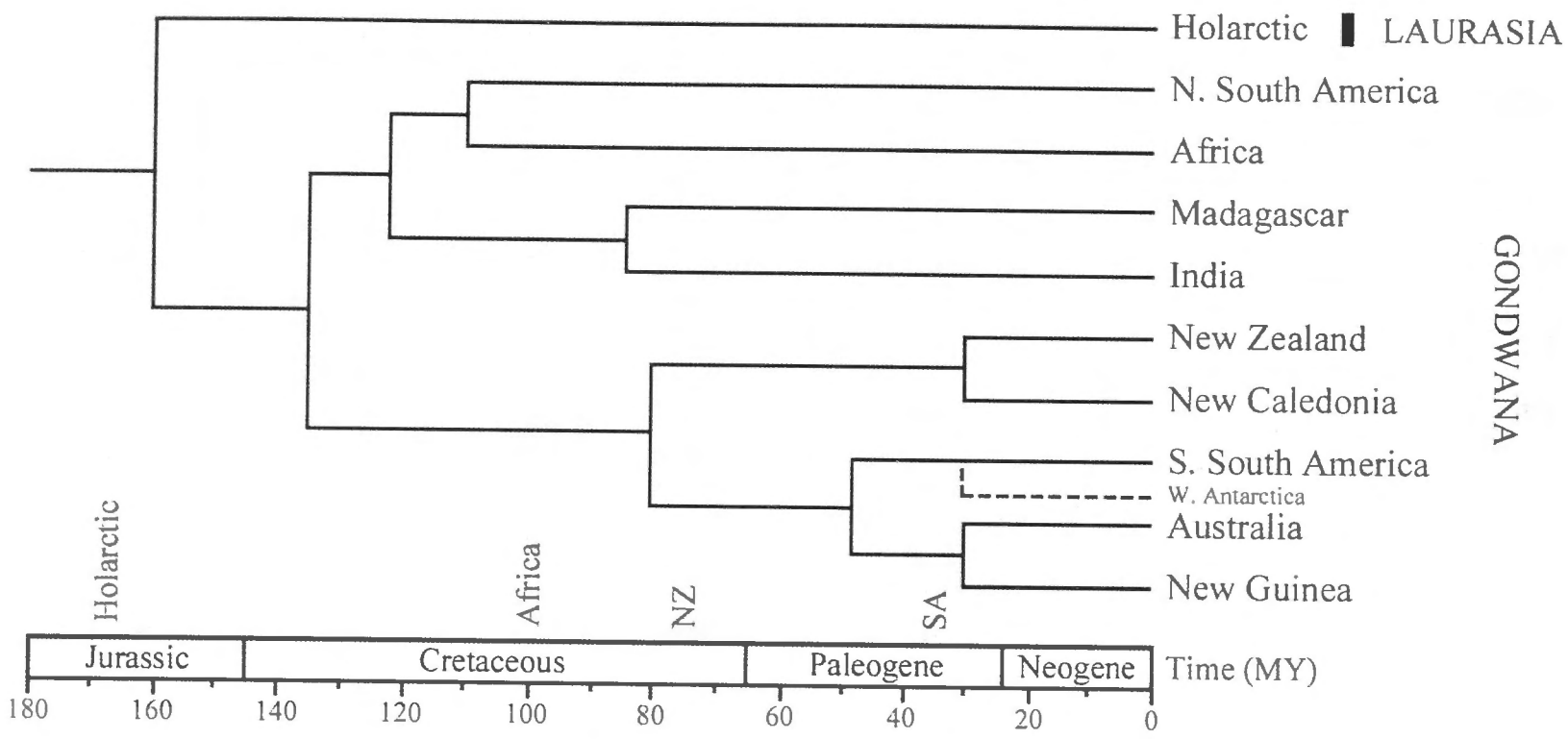


Figure 5: Paleogeographic relationships and temporal division of the Gondwanan landmasses presented by Sanmartín and Ronquist (2004: modified from figure 1, p. 217), including the confidence intervals (colour bars) for the complete separation of the major continents (Crisp *et al.* 2011; Sanmartín and Ronquist 2004). MY, million years; NZ, New Zealand; SA, South America.

Such significant geographical events have ultimately influenced the current distributions of many animal and plant taxa (Cranston *et al.* 2010, 2012; Crisp *et al.* 2011; Sanmartín and Ronquist 2004; Waters and Craw 2006). These Gondwanan patterns of biogeography are often reflected in the phylogenetic structure of austral organisms (Cranston *et al.* 2010, 2012; Crisp *et al.* 2011; Sanmartín and Ronquist 2004). The classic southern Gondwanan pattern often involves African taxa diverging from the sister clade containing the remainder of continental taxa, followed by the New Zealand taxa diverging from the sister group of Australian and South American taxa (Figure 6; Crisp *et al.* 2011; Sanmartín and Ronquist 2004).

Biogeographic radiation patterns can also be explained by the results of divergence time estimation (Crisp *et al.* 2011; Knapp *et al.* 2007). This is particularly useful in determining if colonisation of landmasses is caused by ancient vicariance or more recently by long distance dispersal. According to Sanmartín and Ronquist (2004), many Gondwanan groups, such as the marsupials, are poor dispersers across large geographical barriers and their current biogeography is a result of vicariance. Sanmartín and Ronquist (2004) also demonstrated a well-supported vicariant radiation for a myriad of insects across Africa, Australia, New Zealand and South America, including the

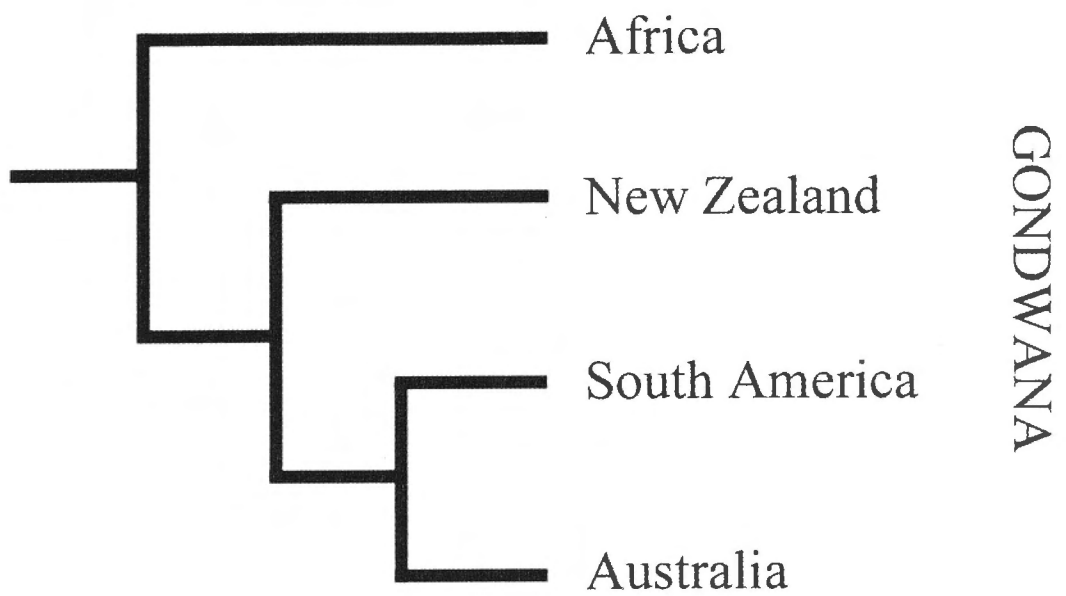


Figure 6: The classic southern Gondwana biogeographic pattern frequently exhibited in austral taxa (Sanmartín and Ronquist 2004: modified from figure 3, p. 220).

Diptera families Chironomidae, Orthocladiinae, Apioceridae, Mydidae and Mycetophilidae. Divergence time estimation can identify vicariant events in a time-calibrated phylogeny, when the divergences of the geographical clades correspond to the events of geographical isolation (Figure 7; Crisp *et al.* 2011; Sanmartín and Ronquist 2004). Alternatively, long distance dispersal can be identified if the divergences of the geographical clades do not correspond to the events of geological isolation (Figure 7; Crisp *et al.* 2011; Sanmartín and Ronquist 2004).

Waters and Craw (2006) stated that vicariance and long distance dispersal are not mutually exclusive events, as more recent dispersal of organisms can override genetic signals of ancient vicariance, particularly for Australian taxa migrating to New Zealand. Moreover, Cranston *et al.* (2010, 2012) and Krosch *et al.* (2011) independently demonstrated, using divergence time estimation, that the Gondwanan pattern in the current biogeography of the Chironomidae was formed by both vicariance and long distance dispersal. Currently the diversification and global radiation patterns of the Tabanidae remain unknown.

1.9 Objectives

The systematics of the Scionini is thus unclear. The taxonomy of the tribe is currently hindered by the limited availability of reliable morphological characters and inadequate diagnoses for many genera. The utility of molecular markers, including mitochondrial

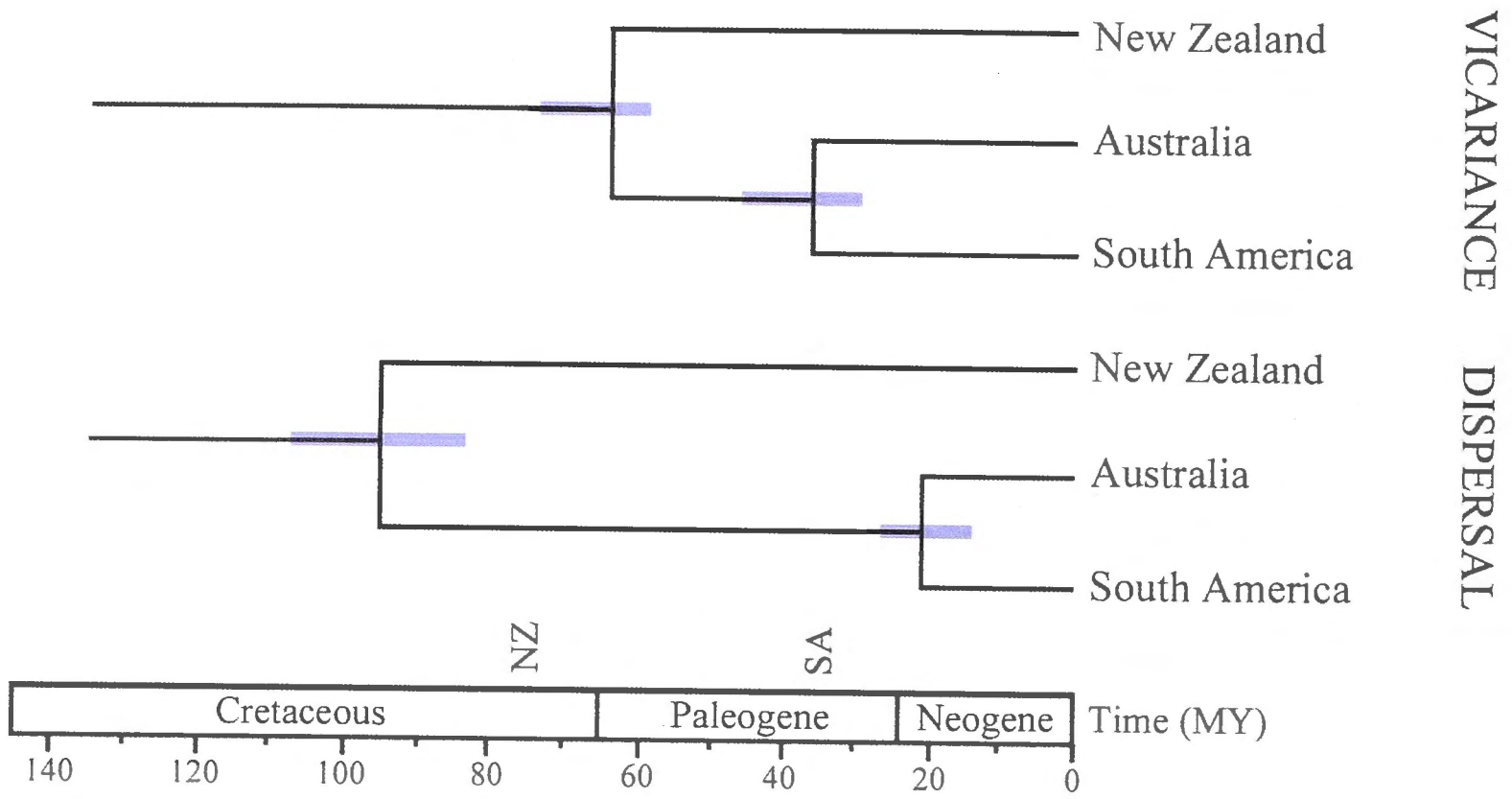


Figure 7: Scenarios of vicariance and long distance dispersal in a time-calibrated phylogeny provided by divergence time estimation, including the confidence intervals for the separation of New Zealand (NZ) and South America (SA) from the remainder of Gondwana. Vicariance is a possible causal process when the confidence interval of the node of interest overlaps with the geological timing of fragmentation. Alternatively, long distance dispersal cannot be rejected when the confidence interval of the node of interest does not overlap with the geological timing of fragmentation (adapted from Crisp *et al.* 2011; figure 1, p. 69). MY, million years.

(COI and COII), ribosomal (28S) and nuclear genes (AATS and CAD), has been previously demonstrated to reconstruct the evolutionary histories of the Diptera, including some genera of the Tabanidae, and may prove useful for studying the phylogenetic relationships of the Scionini. Given the presence of reliable Tabanidae fossils and the current distribution of the Scionini, divergence time estimation may provide novel insights into the global diversification patterns of the tribe with respect to the ancient fragmentation of Gondwana.

Therefore, this thesis aims to:

1.10.1 *Update the species-level taxonomy of the Australasian Scionini*

New material has accumulated in Australian and New Zealand museum collections since the last major revision of the Scionini published over 50 years ago, corresponding to several new species and genera. These new taxa will be identified, described and

illustrated, as well as updating or developing novel taxonomic keys to include all described species. This will ultimately aid in the prompt morphological identification of material for future workers.

Relevant chapters:

III. Lessard B.D. and D.K. Yeates. 2011. New species of the Australian horse fly subgenus *Scaptia* (*Plinthina*) (Diptera: Tabanidae), including species descriptions and a revised key. *Australian Journal of Entomology* **50:** 241-252

IV. Lessard B.D. and D.K. Yeates. 2012a. *Anzomyia* (Diptera: Tabanidae: Pangoniinae: Scionini): a new genus of Australian and New Zealand horse fly, including the description of three new species. *Insect Systematics and Evolution* **43:** 101-116

V. Lessard B.D. and D.K. Yeates. 2012b. Seven new species of the southern hemisphere horse fly subgenus *Scaptia* (*Pseudoscione*) (Diptera: Tabanidae), including descriptions and a revised key. *Journal of Medical Entomology* **49:** 1206-1225.

VI. Lessard B.D. and D.K. Yeates. 2013. New species of the Australian horse fly subgenera *Scaptia* (*Scaptia*) Walker, 1850 and *Scaptia* (*Myioscaptia*) Mackerras, 1955 (Diptera: Tabanidae). *Zootaxa* **3680:** 118-129.

1.10.2 *Construct the first phylogenetic hypothesis for the Scionini using molecular genes*

Previous studies have shown the utility of molecular data in reconstructing the evolutionary history of the Tabanidae. The phylogenetic relationships of the Scionini remain unknown, which is undesirable given the ecological and medical importance of the tribe. Previously molecular studies have demonstrated the utility of mitochondrial (COI), ribosomal (28S) and nuclear (AATS and CAD) genetic markers in resolving the systematics of the Tabanidae, which will be employed in the current study to reconstruct the phylogenetic relationships of the Scionini, with a particular focus on the widest spread genus *Scaptia*. Molecular analysis will also highlight any groups that may require subsequent taxonomic revision.

Relevant chapter:

VII. Lessard B.D, Cameron S.L., Bayless, K.M., Wiegmann B.M. and D.K. Yeates. 2013. The evolution and biogeography of the austral horse fly tribe Scionini (Diptera: Tabanidae: Pangoniinae) inferred from multiple mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* **68:** 516-540.

1.10.3 *Formally revise the taxonomy of the Scionini*

The taxonomy of the Scionini has been historically challenging given the difficulties associated with morphological uniformity, the expansive distribution hampering adequate collection of fresh material for examination, and previously disjointed efforts by international taxonomists spanning several generations. The tribe Scionini will be taxonomically revised using both morphological evidence and the molecular data obtained in Objective 2. All genera will be redescribed, illustrated and provided with information regarding the number of recognised species, distribution, feeding habits and larval stages if known.

Relevant chapter:

VIII. Lessard B.D. 2014. Revision of the austral horse fly tribe Scionini (Diptera: Tabanidae). *Austral Entomology* (in press).

1.10.4 *Assess the global biogeographical patterns of the Scionini*

Divergence time estimation and the fossil record will be combined to place current biogeographical radiation patterns of the Scionini in a temporal context. Divergence time estimation will assess whether the sequential fragmentation of Gondwana has influenced the current biogeography of the tribe. This method may also identify patterns of vicariance or long distance dispersal, as well as providing novel insights into the origin of the tribe.

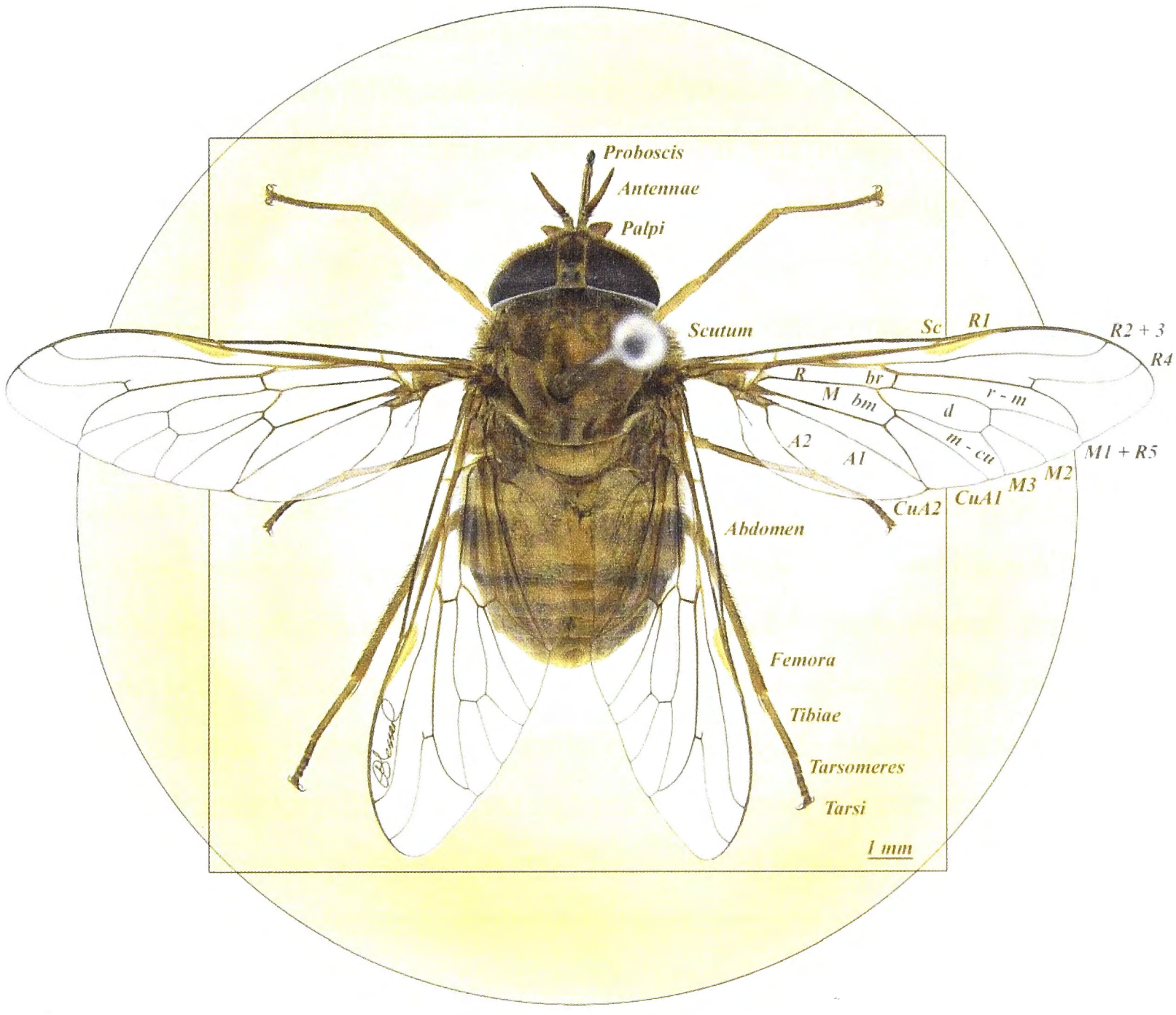
Relevant chapter:

VII. Lessard B.D, Cameron S.L., Bayless, K.M., Wiegmann B.M. and D.K. Yeates. 2013. The evolution and biogeography of the austral horse fly tribe Scionini

(Diptera: Tabanidae: Pangoniinae) inferred from multiple mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* **68:** 516-540.

This thesis is presented as a series of journal articles either published or submitted to peer-reviewed scientific journals. Figures and Tables are presented in the published form and are preceded with the number of the relevant chapter in the Lists of Tables, Figures and Keys (i.e. Figure 4 of Chapter One will become Figure 1.4 as specified in the List of Figures).

Chapter Two



2. General Materials and Methods

The traditional form of species identification has primarily used morphological characters to diagnose species. More recently, molecular techniques have exploited the diversity of nucleotide sequences to identify species, an approach that is considered advantageous due to the statistical support provided by phylogenetic analyses. The purpose of this chapter is to justify the choices of methods made over the duration of the thesis. It will also outline the current practices for traditional morphology-based taxonomy as well as contemporary molecular techniques, including phylogenetic analyses and divergence time estimation. More detailed explanations of the protocols used are presented in the respective chapters.

2.1 Morphological classification and taxonomy

External morphological characters have been traditionally used for describing genera, subgenera and species of the Scionini (Coscarón and Wilkerson 1985; Coscarón and Gonzalez 2001; Coscarón and Iide 2003; Mackerras 1955, 1957, 1960, 1961, 1964; Oldroyd 1947; Wilkerson and Coscarón 1984). The majority of these workers have not found genital characters informative for species-level descriptions and are generally unobserved. Consequently, emphasis has been placed on coloration patterns of the body and wings, in addition to specimen size, which have primarily been used to delimit and identify species. This is exemplified in Mackerras' (1960, p. 106) diagnosis of the Australian species *Scaptia* (*Psuedoscione*) *calabyi* Mackerras, 1960, which he described as being "a medium-sized, light brown species; with no scutal vittae; light yellowish brown legs, femora darkened at most at extreme base; a single, rather faint, darker marking on wing; weakly banded abdomen; and striking rich yellow thoracic and abdominal hairs. Length 11-13 mm". Coloration is generally accepted as a valid morphological character, although care must be taken to distinguish any fading that may impede species identification. For instance, the Australian species *Scaptia* (*Plinthina*) *binotata* (Latreille, 1812) is considered to be "distinguished from [*Scaptia* (*Plinthina*)] *divisa* by its darker general colour" (Mackerras 1960, p. 135), however, older specimens may be subject to fading, becoming "considerably paler in coloration" and may be wrongly identified as *S.* (*Pl.*) *divisa*. In such cases, consultation with structural features, such as the length and form of the palpi, can provide relief for identification; the palpi are larger and broader in *S.* (*Pl.*) *binotata* than *S.* (*Pl.*) *divisa* (Mackerras 1960) and can therefore be distinguished from each other.

More obvious structural differences in the external morphology are used in the classification of the genera and subgenera of the Scionini. These main diagnostic characters include the bulging or truncation of the face, palpi length, width and presence or absence of a lateral pit, the length and width of the proboscis, and the closure of wing cells R_5 and M_3 (Mackerras 1955, 1960). One of the most reliable morphological characters used to diagnose subgenera is the ratio of the frons index, which measures the diverging or parallel appearance of the frons in females, and is calculated by dividing the length of the vertex to the top of the subcallus by the width of the midlength of the frons (Mackerras 1955). These characters are exemplified in the diagnostic features of the subgenus *Scaptia* (*Pseudoscione*), which is distinguished from other Australian

subgenera by the "frons distinctly diverging; proboscis not shorter than one and a half times head height; palpi less than half length of shaft, usually pointed and with deep lateral concavity, occasionally truncate, sometimes slender" as specified in couplet two of Mackerras' (1960, p. 34) diagnostic key to the Australian Scionini.

Morphological terminology of this thesis will follow the previous work of Mackerras (1955, 1957, 1960, *et al.* 2008). Unfortunately, genitalia will not be examined due to the accepted morphological uniformity among most genera and species (Mackerras 1955, 1960). Specimens will be examined using Zeiss dissecting microscopes (Zeiss, Germany). Photographs of type species will be acquired on a BK Plus Lab System featuring a P-51 Cam lift and an Infinity Optics K2 Long Distance Microscope (Visionary Digital, USA), and compiled using Helicon Focus software (available from http://www.heliconsoft.com). All material for examination is sourced from the following institutions:

AM	Australian Museum, Sydney, NSW, Australia
ANIC	Australian National Insect Collection at CSIRO Ecosystem Sciences, Canberra, ACT, Australia
BYU	Brigham Young University, Utah, USA
ERM-LUNZ	Entomology Research Museum, Lincoln University, Canterbury, New Zealand
GDCD	Greg Daniels Private Collection, Brisbane, Qld, Australia (now integrated into AM and QM)
MNZ	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand
NCSU	North Carolina State University, Raleigh, North Carolina, USA
NMH	The Natural History Museum, London, United Kingdom
QDPI	Queensland Department of Primary Industries, Indooroopilly, Qld, Australia
QM	Queensland Museum, Brisbane, Qld, Australia
UQIC	University of Queensland Insect Collection, Brisbane, Qld, Australia
USP	University of São Paulo, Ribeirão Preto, Brazil
SAM	South Australian Museum, Adelaide, SA, Australia
SI	Smithsonian Institute, Suitland, Maryland, USA
WAM	Western Australian Museum, Perth, WA, Australia

2.2 Molecular techniques and phylogeny

The utility of contemporary molecular techniques has been previously demonstrated in reconstructing the phylogenetic relationships of the Tabanidae, excluding the Scionini (Morita 2008; Wiegmann *et al.* 2000). Moreover, molecular techniques can quantifiably assess traditional morphology-based classification schemes and test the taxonomic hypotheses for subfamily, genus and species levels (Morita 2008). Such molecular techniques are expected to be useful in overcoming the morphological and taxonomic challenges associated with the Scionini. Consultation with the literature has provided several candidates for genetic markers that may be useful for reconstructing the phylogenetic history of the Scionini, including mitochondrial and nuclear genes.

2.2.1 Mitochondrial gene markers

The rapid mutation rates of mitochondrial genes have recently been exploited for the use of species level taxonomy of the Diptera. Cytochrome Oxidase is found in the inner mitochondrial membrane and is a key respiratory enzyme for electron transport (Lunt *et al.* 1996). Based on the large size and composition of highly variable and conserved regions, many authors have demonstrated the ease and utility of Cytochrome Oxidase Subunit One (COI) and/or Subunit Two (COII) for reconstructing the evolutionary history of the Tabanidae (Morita 2008; Wiegmann *et al.* 2011) and other Diptera families, including the Acroceridae (Winterton *et al.* 2007), Agromyzidae (Winkler *et al.* 2009), Chironomidae (Cranston *et al.* 2010, 2012; Krosch *et al.* 2011, 2012), Phoridae (Smith and Brown 2008), Scepsidae (Laamanen *et al.* 2005), in addition to the members of the superfamilies Hippoboscoidea (Peterson *et al.* 2007) and Muscoidea (Kutty *et al.* 2008; Lessard *et al.* 2009; Nelson *et al.* 2007; Schuehli *et al.* 2004). Moreover, the popularity of COI and COII as phylogenetic markers is attributed to the abundance of available universal primers specified in the literature (Lui and Beckenbach 1992; Simon *et al.* 1994; Whiting 2002).

2.2.2 Nuclear gene markers

Nuclear protein-coding genes are generally slower to evolve than mitochondrial genes and can therefore provide additional phylogenetic signal at higher taxonomic ranks, including family, subfamily and genus levels (Morita 2008; Moulton and Wiegmann 2004; Wiegmann *et al.* 2011). Based on the literature, there appear to be three suitable nuclear genes commonly used by Diptera systematists, including CAD, AATS and 28S. The carbamoyl-phosphate synthetase (CPS) domain of carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD) gene is responsible for encoding the first three enzymatic activities of the de novo pyrimidine biosynthetic pathway (Moulton and Wiegmann 2004). CAD provides considerate phylogenetic signal at higher taxonomic levels because the gene is slowly evolving, ubiquitous and present as a single copy compared to mitochondrial genes (Moulton and Wiegmann 2004). Several different workers have demonstrated the utility of CAD in resolving the phylogenetic relationships of the Tabanidae (Wiegmann *et al.* 2011; Morita 2008) and other Diptera (Bertone *et al.* 2008; Cameron *et al.* 2007; Wiegmann *et al.* 2009), including the families Acroceridae (Winterton *et al.* 2007), Agromyzidae (Winkler *et al.* 2009), Asilidae (Dikow 2009), Chironomidae (Cranston *et al.* 2010, 2012; Krosch *et al.* 2011), and Phoridae (Smith and Brown 2008), in addition to members of the superfamiles Asiloidea (Trautwein *et al.* 2010), Empidoidea (Moulton and Wiegmann 2007), Hippoboscoidea (Petersen *et al.* 2007) and Muscoidea (Kutty *et al.* 2008; Schuehli *et al.* 2004). Subsequently, several preexisting primers have been developed for the amplification and sequencing of CAD (Moulton and Wiegmann 2004).

Alanyl-tRNA synthetase (AATS) is another nuclear protein-coding gene and class of aminoacyl-tRNA synthetases that regulates the attachment of the amino acid alanine to the 3'-end of $tRNA^{Ala}$, in addition to hydrolysing mischarged serine and Gly-$tRNA^{Ala}$ molecules (Sokabe *et al.* 2009). Based on the composition of highly variable and conserved regions, several workers have found AATS to be phylogenetically informative for the Diptera (Dikow 2009; Wiegmann *et al.* 2009, 2011). Similarly, the 28S ribosomal gene contains slowly evolving regions and provides sufficient phylogenetic signal for reconstructing subfamily and genus level relationships for the Tabanidae (Wiegmann *et al.* 2000, 2003, 2011) and other Diptera (Bertone *et al.* 2008; Friedrich and Tautz 1997), including the families Acroceridae (Winterton *et al.* 2007), Asilidae (Dikow 2009), Chironomidae (Cranston *et al.* 2010; Krosch *et al.* 2011), Phoridae (Smith and Brown

2008), Stratiomyidae (Brammer and von Dohlen 2006) and Therevidae (Yang *et al.* 2000), in addition to members of the superfamilies Asiloidea (Trautwein *et al.* 2010), Empidoidea (Moulton and Wiegmann 2007), Hippoboscoidea (Petersen *et al.* 2007) and Muscoidea (Kutty *et al.* 2008). Consequently, several universal primers specific to the Diptera are available for the amplification and sequencing of the 28S gene.

2.3 Phylogenetic analysis

In modern systematics, phylogenetic analysis is used to reconstruct the evolutionary branching patterns of organisms by measuring the degree of genetic variation between different taxonomic groups. Phylogenetic analysis can also measure the support of each evolutionary branch, providing an objective statement regarding the strength of phylogenetic groupings in the form of bootstrap support values (Stamatakis *et al.* 2008) or posterior probabilities (Huelsenbeck and Ronquist 2001, 2003). Consultation with the literature reveals two commonly accepted methods used to reconstruct phylogenetic relationships of taxa, including Bayesian and maximum likelihood methods. A third method, Parsimony, is also available but has been criticised as containing methodological impediments, such as long branch attraction and exclusion of faster evolving third codon positions, which can skew phylogenetic results (Bergsten 2005). Therefore, Parsimony will be excluded in the current study.

2.3.1 Maximum likelihood

Maximum likelihood incorporates a model of substitution and likelihood ratio tests to determine if changes to a particular parameter provide a significant improvement in the likelihood of a phylogenetic tree (Huelsenbeck and Crandall 1997). The tree with the best score is selected and provided as the most likely phylogenetic relationship (Huelsenbeck and Crandall 1997). Previously, maximum likelihood inference was considered to be slow due to the "algorithmic complexity and the high-computational cost" of analyses (Stamatakis 2006, p. 2688), however, more recent programs such as RAxML have been developed with more rapid and reliable bootstrapping methods for maximum likelihood inference of molecular data (Stamatakis *et al.* 2008). Maximum likelihood based analyses have been useful in resolving the phylogenetic relationships of the Tabanidae (Morita

2008; Wiegmann *et al.* 2000) and other Diptera (Bertone *et al.* 2008; Cameron *et al.* 2007; Cranston *et al.* 2010, 2012; Krosch *et al.* 2011; Moulton and Wiegmann 2007; Wiegmann *et al.* 2003, 2011; Winkler *et al.* 2009), and will therefore be employed in this study.

2.3.2 Bayesian inference

As an alternative to maximum likelihood, Bayesian inference is used to provide the most statistically supported phylogenetic tree by incorporating posterior probabilities (Huelsenbeck and Ronquist 2001). The commonly used program MrBayes performs Bayesian inference using the Markov chain Monte Carlo (MCMC) to approximate the posterior probabilities using a dataset that can contain both molecular and morphological data (Huelsenbeck and Ronquist 2001). An advantage of Bayesian inference is that datasets containing multiple markers can be partitioned into subsets (such as independent genes) and analysed under various evolutionary models (Ronquist and Huelsenbeck 2003). Bayesian inference of multiple genetic markers has been used by several workers studying the evolutionary relationships of the Tabanidae (Morita 2008; Wiegmann *et al.* 2003) and other Diptera (Bertone *et al.* 2008; Brammer and von Dohlen 2007; Cameron *et al.* 2007; Cranston *et al.* 2010, 2012; Krosch *et al.* 2011, 2012; Lessard *et al.* 2009; Moulton and Wiegmann 2007; Petersen *et al.* 2007; Wiegmann *et al.* 2011; Winkler *et al.* 2009; Winterton *et al.* 2007). Bayesian inference is useful not only for assessing taxonomic relationships of organisms, but can also be used to estimate divergence times of lineages.

2.4 BEAST and divergence time estimation

Bayesian Evolutionary Analysis Sampling Trees (BEAST) is a widely used statistical program that estimates divergence times of lineages by combining a dataset, usually in the form of molecular data, with temporal information, such as fossil data, to provide a statistically supported time-calibrated phylogenetic tree (Drummond and Rambaut 2007). Similar to MrBayes, BEAST uses Bayesian inference with the MCMC to reconstruct phylogenetic histories by integrating a large number of evolutionary models in the analysis, including substitution models, relaxed clock models and node calibration models like distribution priors (Drummond and Rambaut 2007). A major advantage of

BEAST analyses is that the phylogeny can be time-calibrated by fixing the age of a node with the known age of a corresponding fossil, provided that the fossil taxon represents the actual common ancestor to that node (Ho and Phillips 2009). The program has been used to provide insights into the temporal diversification of the Neuropterida (Winterton *et al.* 2010) and the Diptera families Agromyzidae (Winkler *et al.* 2009) and Chironomidae (Cranston *et al.* 2010, 2012; Krosch *et al.* 2012).

There are several unique priors that allow BEAST analyses to effectively date the ages of lineage in a phylogenetic analysis. According to Drummond and Rambault (2009), the relaxed molecular clock model is one of the most promising recent advances in molecular phylogenetics because it does not assume a constant rate across a lineage. Instead, it assumes independent rates of evolution on different branches, allowing rates to change over time so that closer related lineages may have similar rates of mutation (Drummond *et al.* 2006, 2007; Ho and Phillips 2009). Furthermore, BEAST allows users to partition the molecular clock models in the analysis so that mitochondrial and nuclear DNA can be given different rates of evolution (Drummond *et al.* 2007), which is more biologically accurate. Relaxed clock models have been used by previous researchers investigating the temporal diversification of the Diptera (Cranston *et al.* 2010, 2012; Krosch *et al.* 2011, 2012; Winkler *et al.* 2009). The Yule tree prior also assumes a constant speciation rate per lineage and is recommended for species-level phylogenies (Drummond *et al.* 2007), and has also been used by multiple researches reconstructing the diversification events of the Diptera (Cranston *et al.* 2010, 2012; Krosch *et al.* 2011, 2012; Winkler *et al.* 2009).

BEAST can also take into account the uncertainty of fossil age with the use of distribution priors, which can assign the highest probability for the nodal age to be somewhat older than the oldest fossil (Ho and Phillips 2007). Soft bound distribution priors are advantageous, as they allow the molecular data to overcome poor fossil calibrations and improve the accuracy of the time-calibrated phylogeny (Ho and Phillips 2009). The effectiveness of soft bound distribution priors has been demonstrated in previous temporal studies of the Diptera (Krosch *et al.* 2011; Winkler *et al.* 2009). Normal distributions are a form of soft bound prior and have a symmetric bidirectional shape, allowing the fossil constraint to be slightly older or younger than the specified nodal age and can account for any uncertainty in the placement of the fossil (Ho and Philips 2009). In the case of the Tabanidae fossil *Eotanoid lordi,* a normal distribution prior of mean 142 MY (SD = 1) would be appropriate for the fossil age of 144-140 MY (Mostovski *et*

al. 2003; Zhang 2012), allowing the constrained node to stray somewhat from the mean nodal age of 142 MY.

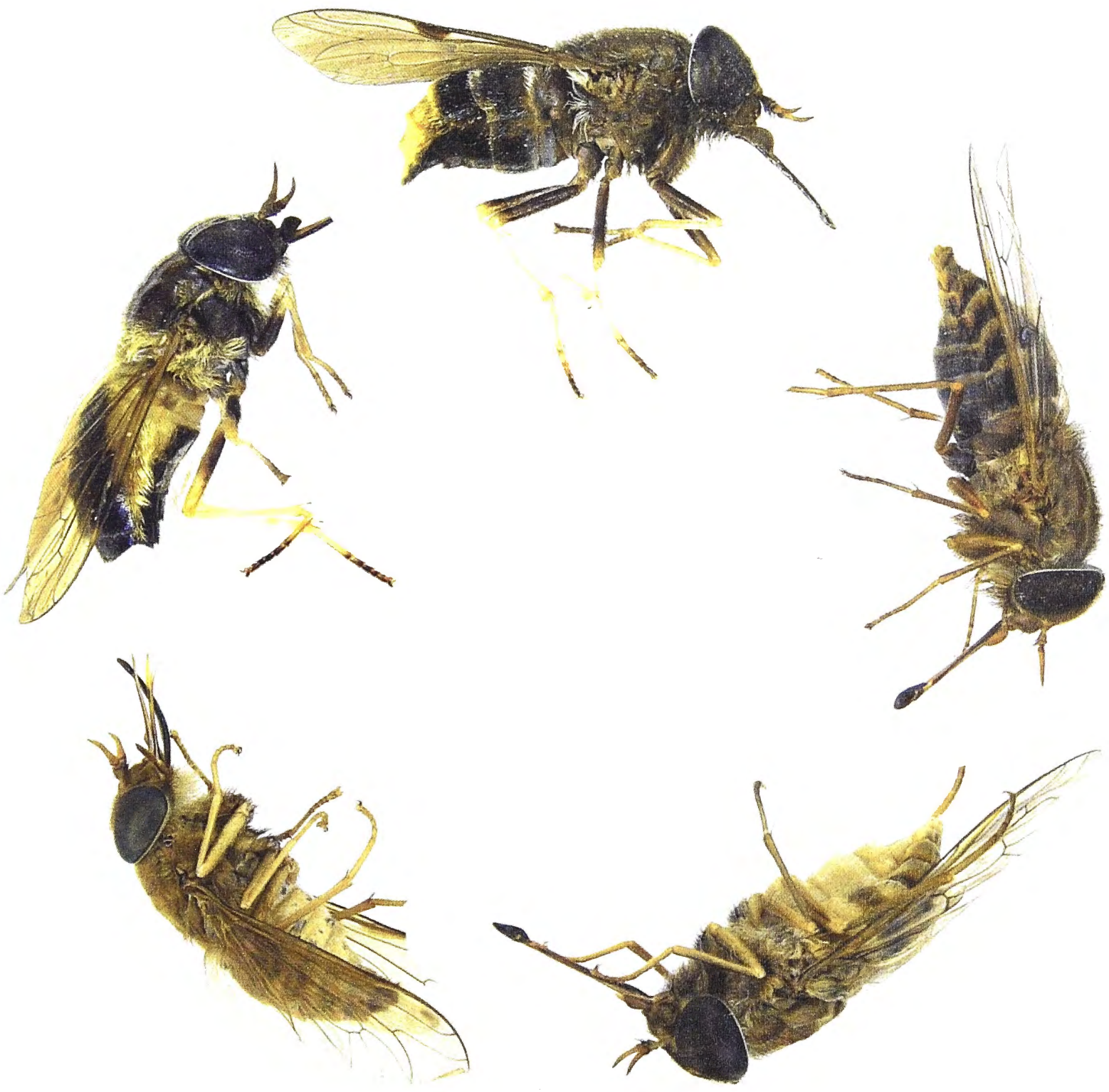
2.5 Conclusions

Traditional morphological characters will be employed to diagnose and describe all new taxa provided in this thesis. This will allow for easier comparisons of the new material with previously described taxa. Conferring with the literature has provided several promising molecular markers that may be useful in reconstructing the phylogenetic relationships of the Scionini, including several mitochondrial (COI and COII) and nuclear (AATS, CAD and 28S) genes. Furthermore, the availability of several universal primers is expected to aid in the prompt amplification and sequencing of those gene regions. Maximum likelihood, Bayesian inference and BEAST analysis are commonly practiced methods in the field of dipteran systematics and will be employed in this study to provide statistically independent hypotheses for the phylogenetic relationships and evolution of the Scionini.

Chapter Three

New species of the Australian horse fly subgenus *Scaptia* (*Plinthina*) (Diptera: Tabanidae), including species descriptions and a revised key

Bryan D. Lessard and David K. Yeates



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New species of the Australian horse fly subgenus *Scaptia (Plinthina)* Walker 1850 (Diptera: Tabanidae), including species descriptions and a revised key

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Abstract Horse flies (Diptera: Tabanidae) are recognised for their medical and veterinary importance, but they also have an important role in pollination. The genus *Scaptia* Walker 1850 contains more than 100 species and comprises seven subgenera with an exclusively southern distribution from Australia, New Zealand, New Guinea and South America. Five new Australian species are described in the subgenus *Plinthina*, which previously comprised only seven species, and an existing key is modified to include the new species, all of which are diagnosed and figured. The new species are: *S. (Plinthina) arnhemensis* **sp.n.** Lessard, *S. (Plinthina) aurifulga* **sp.n.** Lessard, *S. (Plinthina) beyonceae* **sp.n.** Lessard, *S. (Plinthina) nelsonae* **sp.n.** Lessard and *S. (Plinthina) nigripuncta* **sp.n.** Lessard.

Key words Pangoniinae, *Plinthina*, *Scaptia*, Tabanidae, taxonomy.

INTRODUCTION

Almost 4400 species of horse flies have been described (Evenhuis *et al.* 2009) from all biogeographic regions of the world. They are one of the most readily recognised families of Diptera, commonly being considered major pests to both humans and livestock (Mullens 2009). Horse flies are sexually dimorphic in feeding habits as the males feed exclusively on the nectar of flowers, whereas the majority of females act primarily as blood feeders. Some females, such as those belonging to the Australian *Scaptia (Pseudoscione) maculiventris* (Westwood, 1835), alternate between flower and blood feeding (Mackerras 1960). Adults are quite remarkable and important pollinators (Johnson & Morita 2006; Morita 2008), especially for the Australian flora; *Grevillea*, *Melaleuca*, *Leptospermum* and other Myrtaceae are all favoured by horse flies for feeding, consequently leading to their pollination (Mackerras 1960).

Horse flies can also act as intermediate hosts and mechanical vectors for microorganisms responsible for human diseases such as loiasis, tularaemia and even anthrax (Krinsky 1976; Foil 1989). They can also directly infect domestic animals like cattle to cause diseases such as anaplasmosis (Scoles *et al.* 2008) and bovine leukaemia virus (Foil *et al.* 1988), as well as equine infectious anaemia in horses (Foil *et al.* 1984). In Australia, horse flies cause diseases in members of the kangaroo family (Macropodidae), including trypanosomiases (Reid *et al.* 2001) and infections of the filarial nematode *Pelecitus roemeri.* Infections of the latter invade the subcutaneous and intermuscular connective tissues of the animal that can eventually lead to macroscopic lesions (Spratt 1972a,b, 1974a,b, 1975). Spratt has demonstrated that several horse fly species of *Dasybasis* Macquart 1847 and *Tabanus* Linnaeus 1758 commonly host and transmit *P. roemeri.*

The taxonomy of Australian horse flies is remarkably mature, with all but one genus (*Dasybasis*) being revised at species level in the past 60 years. The general lack of definitive characters in the genitalia below a tribal level (Mackerras 1954) means that considerable emphasis has been placed on chaetotaxy and subtle colouration patterns of the body for species level taxonomy (Mackerras 1960). Uses of subtle colour variation is challenging because colours can be modified by collection and preservation techniques, and fade or degrade over time (Mackerras *et al.* 2008; Morita 2008).

Mackerras (1954) revolutionised the classification of the Tabanidae by using male and female genital characters to establish a classification of tribes and subfamilies that is still valid and in use today: Pangoniinae (Pangoniini, Scionini and Philolichini), Chrysopsinae (Bouvieromyiini, Chrysopini and Rhinomyzini), Tabaninae (Diachlorini, Haematopotini and Tabanini) and the Scepsidinae. Furthermore, the monophyly of Tabanidae is well supported by both molecular (Wiegmann *et al.* 2000; Morita 2008) and morphological evidence (Mackerras 1954; Yeates 2002).

There are three tribes within the subfamily Pangoniinae: Pangoniini (Palaearctic, Nearctic, Neotropical and Australasian in distribution), Philolichini (Afrotropical, Oriental and Australasian) and Scionini (Nearctic, Neotropical and Australasian) (Mackerras 1955). The tribe Scionini currently consists of six genera as follows: *Caenopangonia* Kroeber 1930, *Fidena* Walker 1850, *Goniops* Aldrich 1892, *Pityocera*

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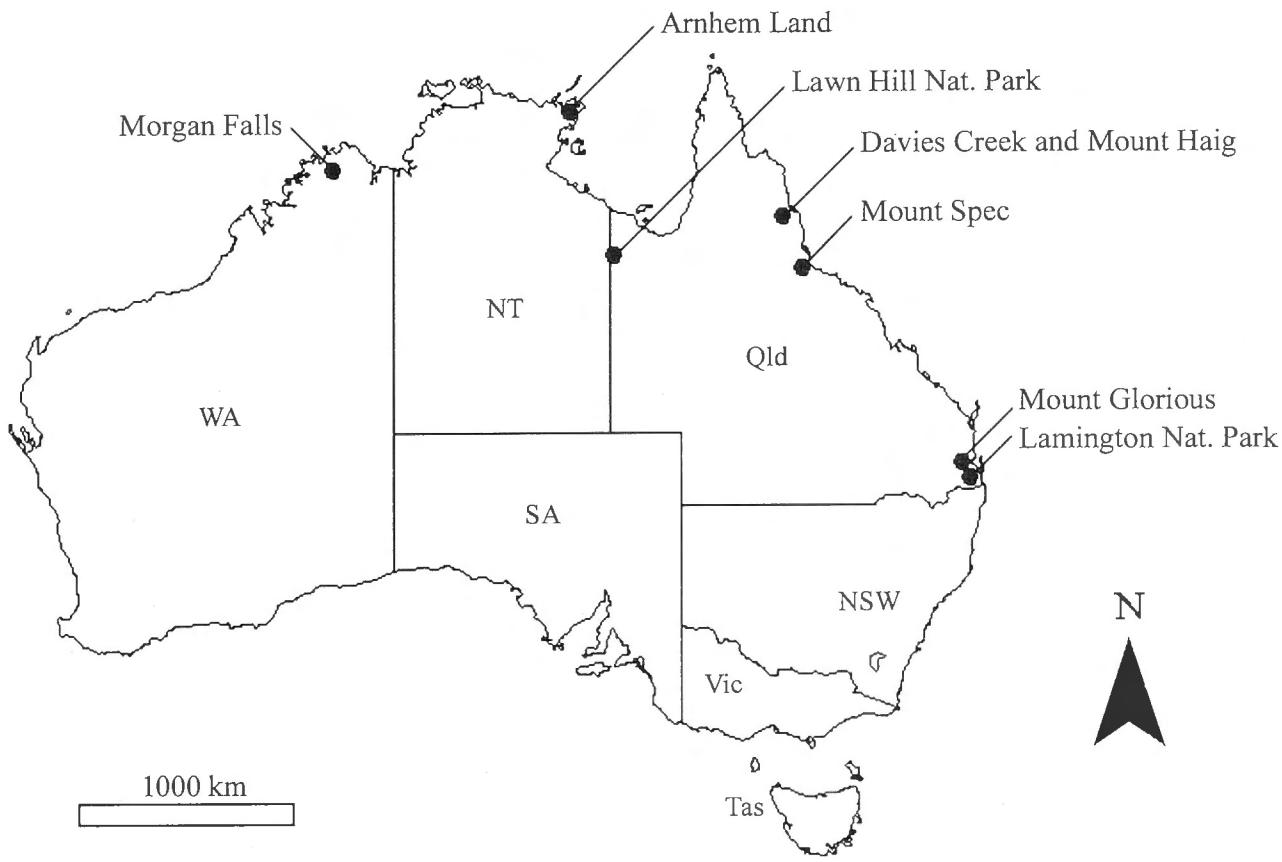

Fig. 1. The distribution of *Scaptia (Plinthina)* species described in this paper, noting the first records of *Scaptia* from the Northern Territory and north-western Australia. NSW, New South Wales; NT, Northern Territory; Qld, Queensland; SA, South Australia; Tas, Tasmania; Vic, Victoria; WA, Western Australia. Background data: Geoscience Australia – Global Map Australia IM 2001, Copyright Commonwealth of Australia.

Giglio-Tos 1896, *Scione* Walker 1850, and the most species-rich genus *Scaptia* Walker 1850.

Scaptia are usually stout, tomentose and hairy, with a more slender proboscis than other Australian Tabanidae (Mackerras 1960). The genus has an exclusively southern hemisphere distribution as it occurs predominantly in Australia, as well as New Zealand, Papua New Guinea and South America (Mackerras 1957; Coscarón & Wilkerson 1985; Daniels 1989; Coscarón & González 2001; Coscarón & Iide 2003; Mackerras 1960; Wilkerson & Coscarón 1984). Seven subgenera have been described and applied to *Scaptia*, being *S. (Lepmia)* Fairchild 1969, *S. (Pseudomelpia)* Enderlein 1922, *S. (Myioscaptia)* Mackerras 1955, *S. (Palimmecomyia)* Taylor 1917, *S. (Plinthina)* Walker 1850, *S. (Pseudoscione)* Lutz, Araujo & Fonseca 1918, and *S. (Scaptia)* Walker 1850, with the latter five occurring in Australia. Although most Australian *Scaptia* species have been described, five new species of subgenus *Plinthina* have accumulated in Australian collections since Mackerras' 1960 revision. Moreover, these species significantly extend the known distribution of *Scaptia* into the Northern Territory and north-western Australia where they were previously thought absent. Here we describe and illustrate these species to double the known size of the subgenus, as well as modifying Mackerras's original key to accommodate all known species of *S. (Plinthina)*.

MATERIALS AND METHODS

Morphological terminology follows Mackerras *et al.* (2008), except for frons index which follows Mackerras (1955). Specimens were examined using Zeiss dissecting microscopes. Photographs were acquired on a Leica M205C microscope using a Leica DF500 camera and Leica Application Suite 3.4.0 software. All material is sourced from the Australian National Insect Collection (ANIC) at CSIRO Ecosystem Sciences, Canberra, ACT, unless otherwise stated. Collection localities are displayed in Figure 1.

A list of abbreviations is as follows:

NT	Northern Territory
Qld	Queensland
QDPI	Queensland Department of Primary Industries, Indooroopilly, Australia
QM	Queensland Museum, Brisbane, Australia
UQIC	University of Queensland Insect Collection, Brisbane, Australia
WA	Western Australia

DESCRIPTIONS

Subgenus *Plinthina* Walker

Plinthina Walker, 1850, p. 10; Ferguson 1924, pp. 253, 256, 1926, p. 299; Mackerras 1955, p. 497. Originally monotypic for *Pangonia macroporum* Macquart, 1838 (= *Pangonia binotata* Latreille, 1812), Kangaroo Island, South Australia.

Diagnosis. The subgeneric diagnosis for *S. (Plinthina)* provided by Mackerras (1960) is as follows: **Female.** Medium-sized (10–14 mm) species, of normal habitus and tomentose patterns, but with the wings usually distinctively marbled, the centres of the cells being darker than along the veins. Frons parallel or slightly diverging. Face moderately projecting, but truncate, proboscis less than one and a quarter times the head height, moderately slender, with relatively small, firm labella. Palpi very short; second segment little, if at all, longer than first, usually thick, rounded apically, and with a large lateral concavity. Wing with cell R_5 closed, and often long-petiolate; cell M_3 open. Eighth sternite often unusually large, fused with lateral edge of ninth tergite. The two halves of the 10th tergite also tend to fuse with each other and with the ninth, evidently a further expression of a need for rigidity in these parts.

Male. Palpi short, slender, cylindrical, obliquely truncate at tip, and with a lateral bare area distally. Hypopygium with aedeagus long; coxite thick and often rigid; style wide, strongly hooked and pointed at tip, and with a zone of conspicuous, short, thick hairs about middle.

Revised key to females of Australian species of *Scaptia (Plinthina)*

1. Wings clear or with inconspicuous marbling; stigma subtle; dorsocentral lines on scutum subtle, not greatly contrasting (Figs 2,3,6,7).....2
   Wings dark brown or grey, or with obvious marbling; stigma obvious; dorsocentral lines on scutum prominent, contrasting (Figs 4,5).....5
2. Palpi thick, with deep lateral concavity (fig. 172; Mackerras 1960); a grey species, with reddish to dark brown markings; frons creamy white. Eastern Australia.....*vertebrata* (Bigot)
   Palpi flattened, with shallow lateral concavity (Fig. 2); golden yellowish brown species; frons brown. Queensland, Northern Territory or northern Western Australia.....3
3. Frons diverging; beard cream (Fig. 7); abdominal markings vague, venter with well-defined black spots. South-east Queensland.....*nigripuncta* Lessard, **sp.n.**
   Frons parallel; beard brown (Figs 2,6); abdomen somewhat banded. Northern Australia.....4
4. Abdomen and venter light golden brown, rotund (Figs 2,3).....*arnhemensis* Lessard, **sp.n.**
   Abdomen and venter dark brown to black, elongated (Fig. 6).....*nelsonae* Lessard, **sp.n.**
5. Petiole of cell R_5 long; palpi small, less than one-third length of proboscis shaft (figs 169–171; Mackerras 1960).....6
   Petiole of cell R_5 short; palpi relatively large, greater or equal to one-third length of proboscis shaft (figs 166–168; Mackerras 1960).....8
6. Palpi pointed, flat with shallow lateral concavity; a black species, with inconspicuous dorsocentral lines on scutum, and anepisternum hairs predominantly black. Western Australia.....*cinerea* (Ricardo)
   Palpi obtuse, thick with deeper lateral concavity; not such dark species, with prominent dorsocentral lines on scutum, and anepisternum hairs predominantly pale.....7
7. Abdomen shining black, with black and ashy hairs. Western Australia.....*subcinerea* Mackerras
   Abdomen with first and second tergites brown, remainder darker, often with indications of a median brown vitta and paler apical bands. Eastern and Western Australia.....*clelandi* (Ferguson)
8. Palpi flat, pointed (fig. 168; Mackerras 1960); an entirely black species, beard largely black. New South Wales.....*nigerrima* Mackerras
   Palpi thick, obtuse (Figs 4,5); not such a dark species with abdomen at most dark brown. Queensland and Western Australia.....9
9. Tibiae completely pale cream to white (Figs 4,5); abdomen with distinct yellow or golden markings; beard black or brownish.....10
   Tibiae brown; abdomen without such markings; beard white.....11
10. Palpi small, less than one-third the length of proboscis shaft (Fig. 4); abdomen with pale yellow lateral stripe tapering apically; femora pale yellow to cream on apical third or more.....*aurifulga* Lessard, **sp.n.**
    Palpi large, greater than or equal to one-third the length of proboscis shaft (Fig. 5); apical tergites and hairs distinctly golden yellow; femora entirely dark brown to black.....*beyonceae* Lessard, **sp.n.**
11. Frons white; scutum with sublateral area dark in colour, prominent, dorsocentral lines pale, conspicuous; abdomen blackish. South and Western Australia.....*binotata* (Latreille)
12. Frons brown; colour of scutum mostly uniform, dorsocentral lines dull, inconspicuous; abdomen dark red-brown. Western Australia.....*divisa* (Walker)

Scaptia (Plinthina) arnhemensis Lessard, sp.n. (Figs 2,3)

Type material. Holotype female, N.E. NT, Arnhem Land, 12°23′15″S 136°36′01″E, 16–27 August 2007, D. Yeates, C. Manchester and S. Winterton (ANIC). Paratype females (6) same data as for Holotype; Paratype females (2), N.E. NT Arnhem Land, Mosquito Creek area, vegetated sand dunes and vine thicket, 12°25′43″S 136°49′55″E, 19–22 August 2007, D. Yeates and C. Manchester; the following Paratype females have the same data as Holotype but with differing coordinates: 1 female 12°23′02″S 136°37′42″E; 1 female 12°23′20″S 136°39′34″E; 2 females 12°23′11″S 136°37′19″E; 3 females 12°15′40″S 136°48′53°E; 4 females 12°16′59″S 136°47′09″E; 18 females 12°20′23″S 136°53′13″E. Paratype male (1), same data as Holotype; Paratype males (2) same data as Holotype but with coordinates 12°16′59″S 136°47′09″E and 12°20′23″S 136°53′13″E.

Other material examined. NT: 1 female, Gulkula Arnhem Bay turnoff via Gove, 15 August 2002, G. Bellis; 1 female, Border Waterhole 15 km W Musselbrook Resource Centre, Lawn Hill National Park, 18°36′44″S 137°59′30″E, 2 May 1996, G. Daniels and M.A. Schneider (UQIC # 97454); Qld: Musselbrook Creek, 19 km NE of Musselbrook Resource Centre Lawn Hill National Park, 18°29′59″S 138°17′01″E, 11 May 1995, G. Daniels and M.A. Schneider (UQIC # 97453); WA: 2 males, Morgan Falls, 15.02°S 126.40°E, 16–17 August 1975, I.F.B. Common and M.S. Upton.

Diagnosis. A small golden brown species (length 9–12 mm) with relatively long and extensively flattened palpi. Wings light grey, superficially clear similar to *S. (Pl.) vertebrata*, but with extremely inconspicuous marbling having a subtle pale edge on the posterior margin of median vein; short petiole to cell R_5. Distinguished from *S. (Pl.) vertebrata* by larger palpi, absence of vittae on abdomen and brown frons.

Fig. 2. *Scaptia (Plinthina) arnhemensis* Lessard, **sp.n.** holotype female: (a) dorsum; (b) side; (c) front; (d) profile.

Female. Length 9–12 mm. **Head**. Dense golden brown hairs. Frons parallel, slightly diverging, index 2.8, with dark brown tomentum. Frons brown, divided into two by paler golden brown areas meeting at median callus; ocellar tubercle slightly raised and greyish, hairs dark brown-black. Subcallus, parafacials and face dark brown with dark brown tomentum. **Antennae**. Scape and pedicle fawn, with dark brown-black hairs; flagellum yellowish brown. **Palpi**. First segment yellowish brown with long black hairs; second segment greatly flattened and extensively shallow bare area, consistent yellowish brown, and less rounded and more tapered shape, marginal hairs short black. Beard pale brown with dense black hairs towards lower margin of parafacials. **Thorax**. Scutum golden brown, with evanescent greyish brown median and dorsocentral vittae, dorsocentral panels darker brown, lateral margins greyish brown; hairs on disc black, white on pronotum. Scutellum pale yellowish brown to cream, hairs black on median and anterior margin, yellow to cream on apical and lateral margins; supra- and post-alar tufts conspicuous mixed pale cream-brown and black. Pleura golden brown to grey, anepisternum hairs predominantly black on dorsum and mixed pale cream to yellowish brown and black posterodorsally,

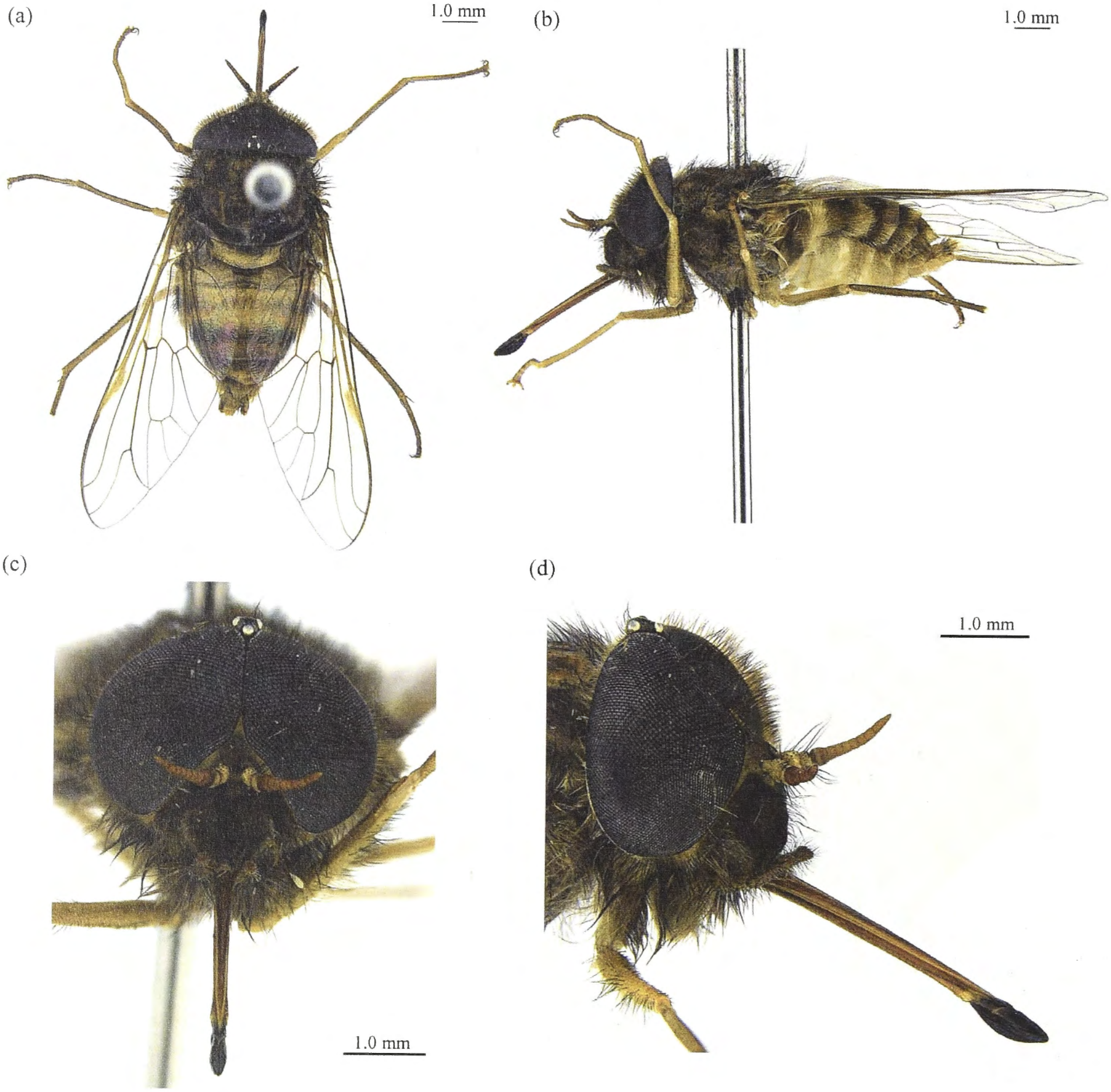

Fig. 3. *Scaptia (Plinthina) arnhemensis* Lessard, **sp.n.** paratype male: (a) dorsum; (b) side; (c) front; (d) profile.

propleural tuft black, mixed yellow-cream and black on katepisternum, mostly yellow-cream elsewhere. **Legs**. Coxa, femora and tarsomeres pale yellowish brown; femora with mixed cream and dark brown hairs, other segments with predominantly dark brown hairs, with short golden brown hairs on ventral surface of all tarsomeres. **Wings**. Lightly grey without conspicuous darker patterns, marbling extremely subtle, with an evanescent pale edge occurring on the posterior length of median vein; stigma subtle, yellowish brown; veins yellowish brown; R_4 angulate, with or without appendix; cell R_5 closed, short-petiolate. **Abdomen**. Golden brown without median vittae, tomentose, with moderately wide darker brown bands at base of tergites, widening slightly laterally; disc hairs on first tergite pale cream-yellow with black median, black on second tergite onwards, densest on darker basal bands, hairs of lateral margins alternating with black basal tufts and pale yellow-cream apical tufts, sparse. **Venter**. Uniformly pale yellowish brown to cream; hairs predominantly pale yellow-cream, with occasional black hairs, often sparse.

Male. Smaller (length 9 mm) and hairier than female. Eyes with upper facets enlarged, reddish brown (pinned), contrasting with small lower and posterior facets that are darker brown. Palpi yellowish brown, rod-like, with small apical dorsal pit with long black hairs. Ocellar tubercle conspicuously raised, slightly grey to dark brown-black, hairs black.

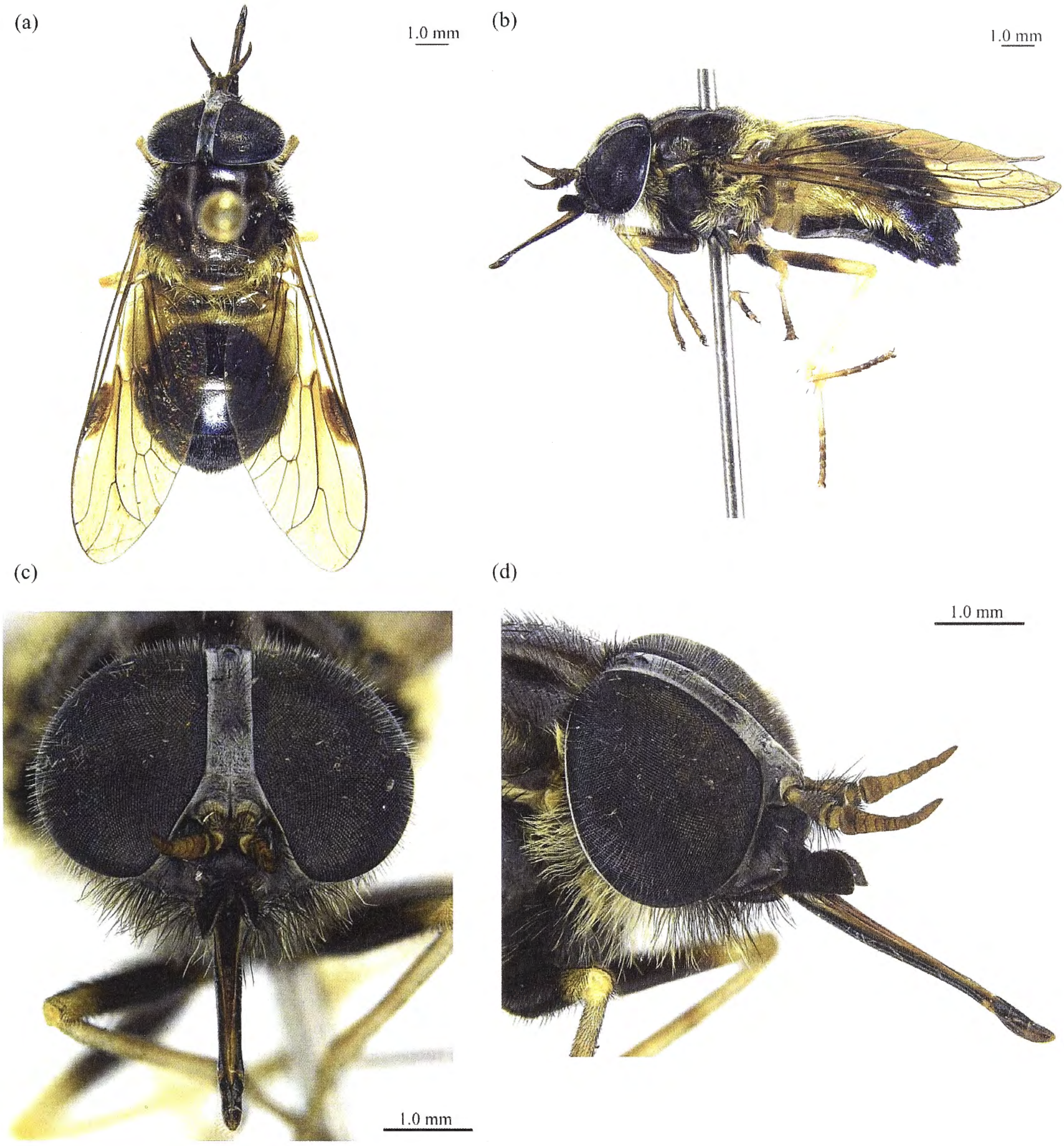

Fig. 4. *Scaptia (Plinthina) aurifulga* Lessard, **sp.n.** holotype female: (a) dorsum; (b) side; (c) front; (d) profile.

Distribution. Arnhem Land, N.E. NT, and the Kimberley region of WA, apparently absent from intervening populated areas such as Darwin (Fig. 1). This species significantly extends the known distribution of *Scaptia* into the Northern Territory and north-western Australia where it was previously thought absent.

Etymology. The specific epithet refers to the type locality.

Scaptia (Plinthina) aurifulga Lessard, sp.n. (Fig. 4)

Type material. Holotype female, N.E. Qld, Davies Creek, Nov, D.H. Colless (ANIC).

Diagnosis. A dark brown species (length 11 mm) with short, rounded and flattened palpi, wings inconspicuously marbled superficially similar to *S. (Pl.) divisa*, with strong stigma and medium petiole to cell R_5. Legs with pale cream to

white tibiae and first tarsomeres, contrasting to dark brown femora that are uniquely pale cream to white on posterior third. Distinguished from all other members of *S. (Plinthina)* by a conspicuous tapered pale yellow stripe on lateral margins of abdomen.

Female. Length 11 mm. **Head**. Eyes with dense brown hairs. Frons parallel, index 3.8, dark brown with obvious wide grey zones along eye margins, broadening at ocellar tubercle; hairs dark brown and sparse; ocellar tubercle slightly raised, greyish brown with hairs black. Subcallus dark brown, with grey zones along eye margins and base of antennae; face and parafacials shiny dark brown, parafacials grey towards eye margins, hairs dark brown. **Antennae**. Scape and pedicel grey to yellowish brown with long black hairs; flagellum uniformly yellowish brown. **Palpi**. First segment predominantly dark brown, hair long black; second dark brown at base and margins, lighter in extensive shallow bare area, marginal hairs short black. Beard mixed cream and brown, with dense black hairs at lower margins of parafacials. **Thorax**. Scutum shining rich brown, greyish brown median line, dorsocentral lines and suture line, as well as pronounced greyish lateral areas; disc hairs black, creamy white on pronotal lobes, pale yellow on median zone in front of scutellum, supra-alar tuft mixed with conspicuous pale yellow and black hair, post-alar tuft dense, conspicuous and pale yellow. Scutellum brown, more yellowish towards posterior margin, hairs pale yellow and long. Pleura greyish brown; hairs predominantly black on anepisternum, pale yellow on propleuron, pale yellow dorsally and black ventrally on katepisternum, and long pale yellow on katatergite. **Legs**. Coxa dark brown with hairs mixed black and pale yellow on fore and mid coxa, and pale yellow on hind coxa. Femora dark brown basally and pale cream to white on posterior third or more; hairs predominantly black, with pale yellow dorsal hairs on mid and hind femora; tibiae and first tarsomere pale cream to white, contrasting to base of femora, hairs pale cream to white, fore tibiae and tarsomere slightly darker than mid and hind tarsomeres, all with black hairs, remainder of tarsomeres yellowish brown, darkening at tarsi with dark brown hairs. **Wings**. Dark brown, marbling inconspicuous with pale edges present on the costal, cubitus, R_1 and medial veins, and posteriorly on R_1 below stigma; stigma dark brown, conspicuous; veins brown; R_4 angulate without appendix; petiole to cell R_5 short. **Abdomen**. Shining dark brown, distinguished from all other members of the subgenus by a striking pale yellow lateral margin stripe beginning broadly on tergite 2 and extending to tergite 4 where it tapers; disc hairs pale yellow on tergite 1 and on pale yellow lateral stripe, black elsewhere, hairs on lateral margin pale yellow on lateral stripe and on tuft of tergite 5, black on apical tergites, lack of golden tomentum on apical tergites. **Venter**. Shining, pale yellow on sternite 1, basal margin of sternite 2, and on lateral margins of sternite 2–4 that form stripe on lateral margins, all with disc hairs pale yellow; remainder of sternites brown with disc hairs black.

Distribution. Known only from Davies Creek, Qld (Fig. 1).

Etymology. This specific epithet derives from the Latin for golden yellow lightning and refers to the striking lateral band present on the abdomen.

Scaptia (Plinthina) beyonceae Lessard, sp.n. (Fig. 5)

Type material. Holotype female, Qld, Mount Haig 21 km N.E.E. of Atherton, Nov, 1981, D.H. Colless (ANIC). Paratype female (1) Qld, 20 km S.E. of Mareeba, Nov, 1981, D.H. Colless; Paratype female (1), Qld, Mount Spec, 15.55S 146.09E, 880 m, 4 November–1 December 1995, M. Cermak.

Other material examined. N Qld: 1 female, 16 km up Davies Creek Road, Mareeba, 2.xii.1984–7.i.1985, Storey and Titmarsh (QDPI).

Diagnosis. A small brown species (length 9 mm), distinguished from all other members of *S. (Plinthina)* by its larger more rounded, broad flattened palpi, conspicuous golden tomentum on tergite four onwards. Legs superficially similar to *S. (Pl.) aurifulga*, but with distinct femora that are almost entirely brown. Wings brownish grey and inconspicuously marbled, superficially similar to *S. (Pl.) divisa*, with pale edges occurring on medial vein and above stigma on R_1; short petiole to R_5.

Female. Length 9 mm. **Head**. Eyes with dense brown hairs. Frons parallel, slightly diverging, index 3, dark brown, most intense near centre, with greyish brown zone along both sides of ocellar tubercle, hairs dark brown; ocellar tubercle slightly raised, dark brown to greyish, hairs black. Subcallus dark brown at centre, greyish towards eye margins and base of antennae; parafacials and face brown to greyish, with dark brown hairs. **Antennae**. Scape and pedicel greyish brown, with long black hairs; flagellum pale yellow brown, darkest at tip and base. **Palpi**. First segment brown, with long black hairs; second larger, flat and rounded, extensive shallow bare area dark brown, marginal hairs short black. Beard predominantly dark greyish brown with black hairs at lower margins of parafacials. **Thorax**. Scutum and scutellum uniformly brown, sublateral areas relatively wide and not sharply differentiated from more greyish brown lateral areas, dorsocentral lines and evanescent median line greyish white and relatively narrow, dorsocentral lines wider and paler near anterior margin and at suture; scutum hairs dark brown to black on disc, greyish white on pronotal lobe, supra- and post-alar tufts mixed creamy white and black; scutellum hairs mixed black and cream. Pleura brown, with black hairs on katepisternum, predominantly black with mixed cream to light brown on anepisternum, katatergite hairs dark brown anteriorly, long cream posteriorly, black elsewhere. **Legs**. Coxae brown with predominantly dark brown to black hairs; femora almost completely brown, with predominantly black hairs, femora contrasting to distinguishable pale cream to white tarsi and first tarsomeres with hairs pale cream to white, remainder of tarsomeres brown, darkening at tarsi, hairs black. **Wings**. Brownish grey, marbling inconspicuous,

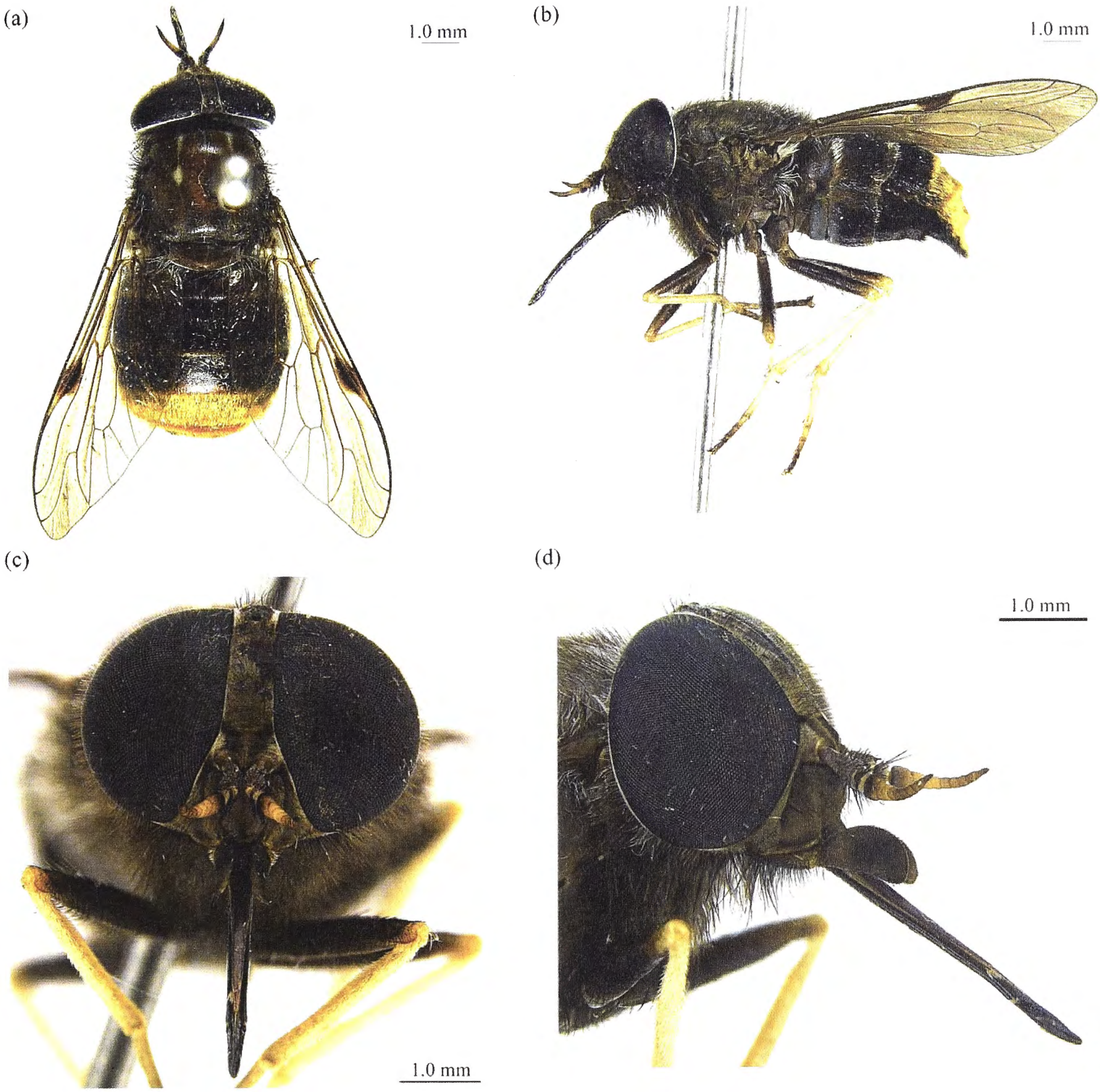

Fig. 5. *Scaptia (Plinthina) beyonceae* Lessard, **sp.n.** holotype female: (a) dorsum; (b) side; (c) front; (d) profile.

with pale edges only occurring on medial vein and base of R_4; stigma prominent dark brown; veins brown; R_4 angulate without appendix; petiole to cell R_5 short. **Abdomen**. Shiny, first three tergites dark brown to black, hair black on disc, white on lateral margins of tergite 1 and apical margin of tergite 2, tergites 4 onward distinctly gold, hairs dense, golden. **Venter**. Dark brown to black, with relatively wide golden brown bands at apical margins of sternites; hairs predominantly black, white towards centre and lateral margins of sternite 2.

Remarks. The Davies Creek specimen appears to be slightly darker and hairier overall, but otherwise similar. This is most likely due to fading or intraspecific variation.

Distribution. N.E. Qld from Mount Haig to Mareeba (Fig. 1).

Etymology. This specific epithet is in honour of the performer Beyoncé.

Scaptia (Plinthina) nelsonae Lessard, sp.n. (Fig. 6)

Type material. Holotype female, WA, Morgan Falls, 15.02S 126.40E, 16–17 August 1975, I.F.B. Common and M.S. Upton (ANIC).

Diagnosis. A small dark brown species (length 11 mm), superficially similar to *S. (Pl.) arnhemensis* but distinguished by its black abdomen and venter, with relatively long, narrow

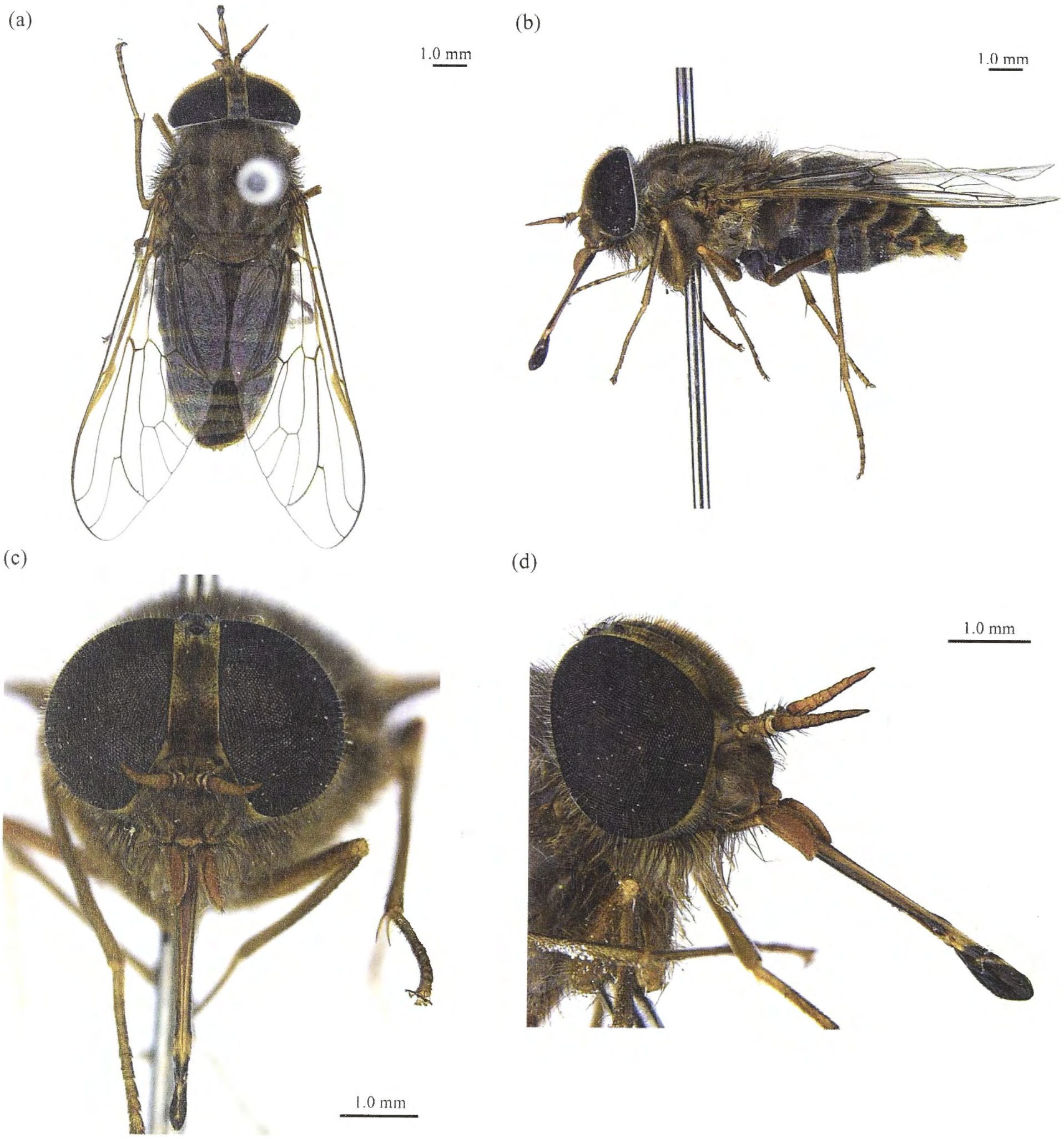

Fig. 6. *Scaptia (Plinthina) nelsonae* Lessard, **sp.n.** holotype female: (a) dorsum; (b) side; (c) front; (d) profile.

pointed palpi that are distinct from other members of the subgenus.

Female. Length 11 mm. **Head**. Eyes with dense brown hairs. Frons parallel, index 2.7, brown with lighter fawn around eye margins, tomentum brown; ocellar tubercle raised, blackish grey with dark brown hairs. Subcallus and face brown, parafacials greyish brown with fawn along eye margins, face and parafacials with dark brown hairs. **Antennae**. Scape and pedicel fawn with dark brown hairs; flagellum consistent yellowish brown. Palpi first segment yellowish brown with long dark brown hairs; second yellowish brown, relatively long, pointed at the tip being the narrowest for the subgenus, marginal hairs short black. Beard cream to light brown, with dark brown hairs at lower margins of parafacials. **Thorax**. Scutum brown, with pale greyish brown evanescent vittae on median and dorsocentral lines, more greyish towards lateral margins; hairs on disc brown, fairly long, white on pronotum, supra-alar tuft mixed cream and dark brown, post-alar tuft cream anteriorly and dark brown posteriorly. Pleura greyish

brown; hairs predominantly cream, with mixed cream and dark brown tufts on anepisternum and dark brown hairs ventrally on katepisternum. **Legs**. Fore and mid coxa greyish brown, hind coxa black; fore and mid legs light brown, darker brown in hind legs; femora hairs mostly cream to light yellowish brown and long, with shorter black hairs posterodorsally, hairs short and densely black dorsally on tibia and tarsomeres, golden brown ventrally. **Wings**. Light grey with less noticeable marbling, pale edges most pronounced around discal cell and median vein; stigma less prominent, yellowish brown; veins brown; R_4 angulate with short appendix; cell R_5 short-petiolate. **Abdomen**. Slightly elongated and narrow, mainly black with brown intrusions; disc hairs black medially and blonde towards lateral margins on tergite 1, black on tergites 2 onward, with short blonde hairs on apical margins, lateral margins mixed blonde and black. Venter black with brown intrusions, hairs mostly blonde, black on apical sternites.

Distribution. Known only from the holotype from the Kimberley, Western Australia (Fig. 1). This species also significantly extends the known distribution of *Scaptia* into north-western Australia.

Etymology. This specific epithet is in honour of Dr Leigh Nelson for her contribution to Dipterology.

Scaptia (Plinthina) nigripuncta Lessard, sp.n. (Fig. 7)

Type material. Holotype female, S.E. Qld, Lamington National Park, 28.234°S 153.141°E, 14–24 January 2007, C. Lambkin and N. Starick (QM #T165588) (ANIC). Paratype female (1) Lamington National Park, Qld, 28.192°S 153.124°E, 14–24 January 2007, C. Lambkin and N. Starick (QM #T165589); Paratype female (1) Lamington National Park, Qld, 28.227°S 153.131°E, 14–24 January 2007, C. Lambkin and N. Starick (QM #T165590).

Other material examined. SE Qld: 3 females Mount Glorious, Hiller Property, 27°20′S 152°46′E, 12.xii.1998–28.i.1999, N. Power (QM).

Diagnosis. A small golden yellow-brown species (length 9–11) similar to *S. (Pl.) arnhemensis*, but distinguished by its cream beard, diverging frons, shorter more rounded palpi, dark brownish grey wings, petiole to cell R_5 extremely short, vague abdominal markings, and venter with lateral rows of black markings.

Female. Length 9–11 mm. **Head**. Eyes with dense golden brown hairs. Frons diverging, index 3.3, with dark brown tomentum. Frons lighter golden brown and without being divided into darker zones; ocellar tubercle slightly raised, dark brown with black hairs. Subcallus, parafacials and face golden brown with short brown hairs. **Antennae**. Scape and pedestal fawn with black hairs; flagellum yellowish brown. **Palpi**. First segment golden brown with long black hairs; second segment yellowish brown, extensively flattened, smaller, slightly rounded and less tapered; marginal hairs sparse short black. Beard cream, black hairs at lower margins of parafacials. **Thorax**. Scutum golden yellowish brown, with darker greyish brown vittae on dorsocentral lines, lateral margins and transverse suture, with dorsocentral panels light golden brown; disc hairs mixed with short golden brown and longer black hairs, supra-alar tuft mixed black and blonde to golden brown, post-alar tuft blonde to golden brown anteriorly and black posteriorly. Scutellum greyish brown predominantly with blonde to golden brown hairs. Pleura yellowish brown, with dark brown-black marking on suture between katatergite and katepimeron; pleura hairs predominantly yellowish brown, with mixed yellowish brown and dark brown hairs on anepisternum and katepisternum, cream hairs on propleuron and katatergite. **Legs**. Fore coxa light yellowish brown, pale yellow-cream on mid and hind. Femora pale yellow-cream with long dark brown to black hairs, tibiae and tarsomeres pale yellow-cream, with short dense golden brown hairs. **Wings**. Brownish grey, marbling very subtle with pale edges occurring on median vein and above stigma on vein R_1; stigma brown, less conspicuous; veins yellowish brown; R_4 curved, without appendix; petiole to cell R_5 extremely short, with cell R_5 closing very close to or on wing margin. **Abdomen**. Golden yellowish brown, tomentose, lack of obvious banding, with vague darkening on tergites 2 onwards, most prominent towards median, apical quarter of tergites brown and without dark markings, tergites 6 onwards dark golden brown; disc hairs on first tergite blonde to golden brown at base and dark brown apically, predominantly golden brown on remainder of abdomen, with golden yellow hairs on apical margins of tergite 3 onwards, hairs on lateral margins of abdomen mixed golden brown and dark brown to black. **Venter**. Pale yellow to cream, darker golden brown from sternite 6 onwards, marked with three distinct black lateral rows on both lateral margins and median of sternites 2–5; disc hairs predominantly pale yellow to cream on sternites 1–5, black on sternites 6 onwards.

Remarks. One specimen from Mount Glorious, Qld, is more tomentose and slightly darker brown in shade for the frons, subcallus, parafacials and face. Its palpi are also a darker shade of brown to the rest, and appear to be more rounded and not tapered at all. The scutum colour is duller than others, and the lateral rows of black markings on the venter are less obvious.

Distribution. South-eastern Qld (Fig. 1).

Etymology. This specific epithet is derived from the Latin for black dot and refers to the markings on the venter.

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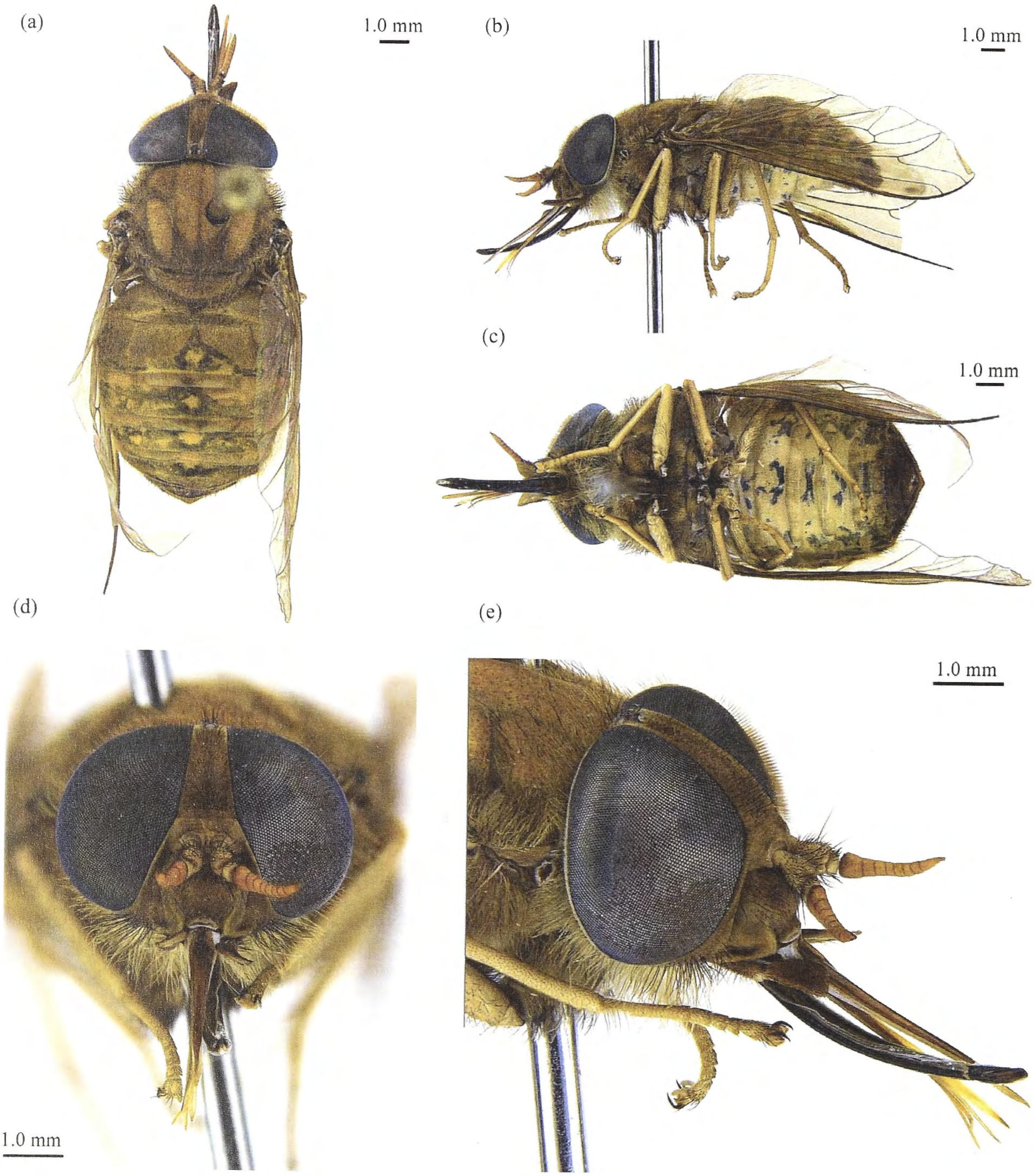

Fig. 7. *Scaptia (Plinthina) nigripuncta* Lessard, **sp.n.** holotype female: (a) dorsum; (b) side; (c) venter; (d) front; (e) profile.

their respective collections and for specimen loans. Ian Mackerras is gratefully acknowledged for providing the foundations for Australian horse fly taxonomy. This paper is a product of NSF Partnerships Enhancing Expertise in Taxonomy (PEET) grant 'Taxonomic, Phylogenetic and Evolutionary Studies of Horse Flies (Diptera: Tabanidae): An Integrated Approach to Systematics Training' (DEB 0731528).

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Chapter Four

Anzomyia (Diptera: Tabanidae: Pangoniinae: Scionini): a new genus of Australian and New Zealand horse fly, including the description of three new species

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Anzomyia (Diptera: Tabanidae: Pangoniinae: Scionini): a new genus of Australian and New Zealand horse fly, including the description of three new species

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Abstract

A new genus of Australian and New Zealand horse fly, *Anzomyia* Lessard, gen.n., is described, with its type species *Anzomyia anomala* (Mackerras) originally placed in the *Scaptia* (Walker, 1850) subgenus *Pseudoscione* (Lutz, 1918). The new genus *Anzomyia* is diagnosed and illustrated, along with the description of three new species. A taxonomic key is also provided to include all known species. The three new species are *Anzomyia chrysomallis* Lessard, sp.n. and *Anzomyia pegasus* Lessard, sp.n. from Australia, and *Anzomyia herculensis* Lessard, sp.n. from New Zealand.

Keywords

Scaptia, *Pseudoscione*, *Copidapha*, *anomala*, descriptive taxonomy, morphology

Introduction

Horse flies (Diptera: Tabanidae) are well known for their blood-sucking behaviour, and are ecologically diverse with almost 4400 extant species described throughout the world (Evenhuis et al. 2009). Through feeding the females of many species are known to transmit diseases to livestock (Foil et al. 1984, 1988; Scoles et al. 2008), some Australian marsupials (Spratt 1972a,b, 1974a,b, 1975; Reid et al. 2001) and even humans (Krinsky 1976; Foil 1989). The family also plays an important role in the pollination of plants (Johnson & Morita 2006; Morita 2008), including *Eucalyptus* and tea tree genus *Leptospermum* in Australia, with the latter also being pollinated by horse flies in New Zealand (Tillyard 1926; Mackerras 1957, 1960).

The monophyly of the Tabanidae is supported by both morphological (Mackerras 1954; Yeates 2002) and molecular data (Wiegmann et al. 2000, 2011; Morita 2008). However, species-level taxonomic research in the family is hampered because both

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sexes have general morphological uniformity in genitalia below the tribal level (Mackerras 1954). Consequently, emphasis has been placed on morphology, especially colour patterns which can be modified overtime due to fading, difference in specimen age, or collection method and curation (Lessard & Yeates 2011; Mackerras et al. 2008; Morita 2008). Nonetheless the taxonomy of the family is fairly stable, with today's classification scheme based on the work of Mackerras (1954) who used genitalia and external characters to divide the family into four subfamilies, with further tribal division: Chrysopsinae (Bouvieromyiini, Chrysopini and Rhinomyzini), Pangoniinae (Mycteromyiini (added by Coscarón & Philip, 1979), Pangoniini, Philolichini and Scionini), Scepsidinae, and, the largest of the subfamilies, Tabaninae (Diachlorini, Haematopotini and Tabanini).

The subfamily Pangoniinae consists of four tribes, the Mycteromyiini (Neotropical in distribution), Pangoniini (Australasian, Nearctic, Neotropical and Palaeartic), Philolichini (Afrotropical, Australasian and Oriental) and the Scionini (Australasian, Nearctic and Neotropical) (Mackerras 1955). The Scionini is further divided into six genera, including *Caenopangonia* Kroeber 1930, *Fidena* Walker 1850, *Goniops* Aldrich 1892, *Pityocera* Giglio-Tos 1896, *Scione* Walker 1850, and, the most species-rich genus, *Scaptia* Walker 1850.

Scaptia are usually stout and hairy flies, with a more slender proboscis than other Australian Tabanidae (Mackerras 1960). The genus has an exclusively southern hemisphere distribution, occurring predominantly in Australia, New Zealand, Papua New Guinea and South America (Oldroyd 1947; Mackerras 1957, 1960, 1961, 1964; Wilkerson and Coscarón 1984; Coscarón and Wilkerson 1985; Daniels 1989; Coscarón and González 2001; Coscarón and Iide 2003; Coscarón and Papavero 2009; Lessard and Yeates 2011). Seven subgenera have been described and applied to *Scaptia*, including *Lepmia* Fairchild 1969 (Brazil), *Pseudomelpia* Enderlein 1922 (Chile), *Myioscaptia* Mackerras 1955 (Australia), *Palimmecomyia* Taylor 1917 (Australia), *Plinthina* Walker 1850 (Australia), *Scaptia* Walker 1850 (Australia, Chile, Peru, Bolivia, Argentina), and *Pseudoscione* Lutz in Lutz, Araujo & Fonseca 1918 (Australia, Argentina, Brazil, Chile, New Guinea and New Zealand).

In the one of the most extensive revisions of the Pangoniinae, Mackerras (1955) referred to one undescribed Australian species as being most similar to *S.* (*Pseudoscione*), based on similarities in the antennal flagellomeres and genitalia, but also sharing the short fleshy proboscis and large, hairy antennal scape, most similar to *S.* (*Pseudomelpia*). It was not until Mackerras' 1960 revision of *Scaptia* when this unnamed species was first described as *Scaptia anomala*. Furthermore, it was identified as an intermediate species closely related to both *S.* (*Scaptia*) and *S.* (*Pseudoscione*), and was provisionally placed within *S.* (*Pseudoscione*), so it would not escape recognition: "*S. anomala* is exceptional, in combing the short proboscis and long palpi of [the subgenus] *Scaptia* with the diverging frons and general appearance of [the subgenus] *Pseudoscione*... a case could be made for establishing [a new subgenus] for *Scaptia*, [being] *S. anomala*, and that may prove to be a proper course when more is known about it." (Mackerras 1960, p. 33). Based on its intermediate anatomical form, Mackerras (1955) hypothesized that *S. anomala* may represent a unique derivation from the ancient

S. (*Pseudoscione*) lineage. He further stated that this species would most likely represent the earliest form of the Scionini, and adapted to nectar feeding of early flowering plants (Mackerras 1960).

Over the last 50 years, new material belonging to the *anomala* group has accumulated in both Australian and New Zealand collections. This is the third paper in a recent series renewing the descriptive work on the Australian Tabanidae (Mackerras et al. 2008; Lessard & Yeates 2011) since Ian Mackerras passed away. The increase in available evidence reinforces Mackerras' suggestion to remove *S. anomala* from its previous position within the genus *Scaptia,* and supports its raising to a new genus *Anzomyia* Lessard, gen.n. in the Scionini. Three new species have also been identified and are described below in the new genus, and an original key is provided to include all known species. Moreover, *Anzomyia* and *S. (Pseudoscione)* are the only two Scionini genera that are distributed in two or more continents in the southern hemisphere.

Materials and Methods

Morphological terminology follows Mackerras et al. (2008). Specimens were examined using Zeiss dissecting microscopes. Photographs were acquired on a BK Plus Lab System featuring aP-51 Cam lift, Infinity Optics K2 Long Distance Microscope, and Helicon Focus software. All material is sourced from the Australian National Insect Collection at CSIRO Ecosystem Sciences, Canberra, ACT, unless otherwise stated. Collection localities are displayed in Figure 1.

Fig. 1 The distribution of *Anzomyia* Lessard, gen.n., displaying species localities from Australia and New Zealand. NSW, New South Wales; NT, Northern Territory; Qld, Queensland; SA, South Australia; Tas, Tasmania; Vic, Victoria; WA, Western Australia.

List of abbreviations:

ACT	Australian Capital Territory
ANIC	Australian National Insect Collection, CSIRO Entomology, Canberra, ACT, Australia
ERM-LUNZ	Entomology Research Museum, Lincoln University, Canterbury, New Zealand
NSW	New South Wales
NZ	New Zealand
Vic	Victoria
WC	Wilson Collection, Melbourne, Vic

Systematics

Family: Tabanidae
Subfamily: Pangoniinae
Tribe: Scionini

Genus *Anzomyia* Lessard, gen.n.

Type species

Scaptia (*Pseudoscione*) *anomala* Mackerras, 1960, Australia, by present designation.

Species included

Anzomyia anomala (Mackerras); *Anzomyia chrysomallis* Lessard, sp.n.; *Anzomyia herculensis* Lessard, sp.n.; *Anzomyia pegasus* Lessard, sp.n.

Diagnosis

Female. Small (length 6-10 mm), dark and hairy species. Frons strongly diverging (index 2.2–2.5). Face truncate to moderately bulging, or relatively projecting (Figs 2–5). Proboscis short, less than the length of the head, thick, with extensively developed labella. Palpi long, usually half the length of the proboscis shaft, very slender, subcylindrical and fusiform, with small apical pits reduced to flat ovals. Scutum with at least indications of vittae. Wings never marbled, usually brown or greyish; stigma brown and subtle; R_4 angulate to slightly curved, without appendix; cell R_5 widely open; cell M_3 always open. Genitalia originally described by Mackerras (1960) as small, with rounded gonophophyses, unchitonised 10th tergite, truncate cerci, lateral arms of the furca rather large, and caudal ends of the spermathecal ducts long, lightly chitonised.

Male. Similar to the female but hairier and somewhat darker (Fig. 5). Eyes with upper facets not obviously enlarged. Palpi shorter and more cylindrical than females. Mackerras (1960) stated that the genitalia are similar to *S.* (*Pseudoscione*) without major structural modifications; style of hypopygium finger-like, rounded at tip. Males are unknown for *An. chrysomallis* and *An. pegasus.*

Distribution

The genus appears to be limited to high altitude mountain regions, such as the Great Dividing Range of southeastern Australia, and southwest of the South Island alpine fault in New Zealand (Fig. 1).

Remarks

There is no information on the biology or feeding habits of *Anzomyia*. The genus is separated from *Scaptia* and other members of the Scionini by its smaller size, dark colouration, strongly diverging frons, short and thick proboscis with an extensively developed labella, and palpi that are slender, subcylindrical, longer than half the length of the proboscis shaft, and with reduced, apical, oval-shaped pits.

Etymology

The name is derived from the Greek *myia,* fly, combined with the Australian and New Zealand distribution of the genus.

Key to females of species of the genus *Anzomyia*

1. Antennae relatively short and thick (Figs 4 and 5); scutum with obvious grey postpronotal lobe contrasting ground colour, and well-defined vittae that exceed suture; wings clouded; abdomen relatively tapered, and with a black apical fringe on tergite three; New Zealand.....*herculensis* Lessard, sp.n.
   Antennae more normal (Fig. 3); scutum with subtle postpronotal lobes concolorous to ground colour, and with indications of vittae limited to anterior area; wings not obviously clouded; abdomen more rounded, with creamy white or golden yellow apical fringes on tergite three; Australia..... 2
2. Frons with golden yellow hairs at base; beard and pleural hairs golden yellow (Fig. 2); scutum grey with a bluish hue; abdomen without obvious apical bands or medial triangles..... *chrysomallis* Lessard, sp.n.
   Frons with predominantly brown hair; beard and pleural hairs grey to creamy white (Fig. 3); scutum brown to black, without bluish hues; abdomen with well pronounced apical brown bands and grey medial triangles..... 3
3. Face noticeably projecting (Fig. 3); palpi longer, usually over half the length of the proboscis shaft; head, thorax and abdomen dark greyish black; scutal vittae less obvious; scutum and abdomen with golden yellow hairs.....
   .....*pegasus* Lessard, sp.n.

Face truncate to bulging (fig. 148 in Mackerras 1960); palpi shorter, usually only half the length of the proboscis shaft; head, thorax and abdomen brown; scutal vittae more pronounced; scutum and abdomen with creamy white to brown hairs..... *anomala* (Mack.)

***Anzomyia anomala* (Mackerras)**

Scaptia (*Pseudoscione*) *anomala* Mackerras, 1960: 118, figs 148–151.

Type specimens

Holotype ♀, Australia, Vic, near Warburton, 4000 ft, 25 Jan 1942, F.E. Wilson (WC). Allotype ♂ (1), Australia, ACT, Mt Gingera, 3 Jan 1951, S.J. Paramonov (ANIC).

Other specimens examined

♀ (1), Australia, NSW, Clyde Mountain, 23 Jan 1960, I.F.B. Common & M.S. Upton (ANIC). ♀ (1), Australia, NSW, Kosciuszko National Park, 1.7 km ENE of Thredbo, over narrow stream in flowering wide grassy creek bed, 36°30'07"S 148°19'02"E GPS, 1380 m, malaise, 3-11 Jan 2002, CL Lambkin & NT Starick (ANIC #29 007019). ♂ (5), Australia, NSW, Mt Imlay National Park, Mt Imlay summit, 52 km SE Bombala, 37°10'49"S 149°44'04"E GPS, 886 m, hand net, 13 Jan 2005, C Lambkin & N Starick (ANIC).

Diagnosis

An appropriate diagnosis was given by Mackerras (1960): a small (length 9–10 mm), dark species, with very slender palpi, grey beard, clear wings, and dull creamy to yellowish apical hairs on abdominal tergites.

Description

Female. Head: Eyes with long, dark brown hairs, relatively sparse on lower facets. Frons diverging to antennae, brown, with long black hairs; ocellar tubercle brown. Subcallus greyish brown, without hairs; parafacials and face creamy grey, both with long mixed black and white hairs; central area of face without hairs. Antennae: Scape and pedicel covered with creamy grey tomentum, and with long black hairs; flagellum creamy grey at extreme base, lighter brown on ventral part of first flagellomere, becoming blackish brown distally. Palpi: Second segment very slender, creamy grey, with a small, oval, depressed, brownish area on distal half, and with long white and some black hairs. Beard greyish white. Thorax: Scutum and scutellum dull, dark brown, with indications of paler dorsocentral lines anteriorly and at suture, and lighter brown anterior margin and lateral areas; disc covered with a mixture of short, appressed, creamy white and longer, more erect, dark ones; notopleural hairs mixed black and greyish cream; supra- and postalar tufts and marginal scutellar hairs long, dull greyish cream. Pleura grey,

with greyish white hairs, a few darker ones on upper anipesternum, and a dense white tuft below wing root. Legs: Femora with pale grey tomentum overlaying a dark brown ground colour, and with greyish white hairs; tibiae and tarsomeres light brown, darkening to blackish brown on apical tarsal segments, with black hairs, which are somewhat bristly on tibiae. Wings: Greyish, with faint brownish staining in costal cell and basally; veins brown; R_4 gently curved, without appendix; cell R_5 widely open. Abdomen: Brownish black, with long black hairs, apical margins of tergites creamy brown, with a fringe of rather dense, creamy hairs, which widen to form indefinite median triangles on first to fifth tergites, marginal creamy hairs longer, but not especially dense. Venter: Grey, apical margins of sternites pale creamy grey, hairs silvery.

Male. Similar to female, but more hairy. Face somewhat darker, with darker hairs; beard rather creamy yellow. Palpi similar to female, but the brown bare area distally is smaller. Pale hairs on scutum and abdominal tergites golden in Victorian specimens, similar to Allotype male. Femora black, with less overlay of pale grey tomentum.

Remarks

A series of five male specimens from Mount Imlay, along with one female from Kosciuszko National Park, have the scutum with less pronounced vittae and denser, dull creamy white hairs, and are darker overall, specifically darker brownish black on the antennae, thorax, legs, and abdomen. We interpret these differences as variation within the species.

Distribution

Southeastern Australia, ranging from the ACT to southern Vic (Fig. 1).

Anzomyia chrysomallis Lessard, sp.n. (Fig. 2)

Type specimen

Holotype ♀, Australia, NSW, Mount Wilson, 30 Dec 1960, D.H. Colless (ANIC).

Diagnosis

A small (length 10 mm), *Calliphora*-like species, distinguished to *An. anomala* by its dark bluish grey scutum, golden yellow to brown palpi that are relatively blunt and flat distally, and distinct golden yellow hairs present on lower margins of the frons, parafacials, antennae, beard, scutum, pleura, femora and abdominal marginal hairs.

Female. Length 10 mm. Head: Eyes with rather dense, long, dark brown hairs. Frons wide and clearly diverging, index 2.4, pale grey, hairs long and brown with and a distinct golden yellow tuft at the lower margin near the subcallus; ocellar tubercle slightly raised, dark greyish brown, with long black hairs. Subcallus pale brownish grey and

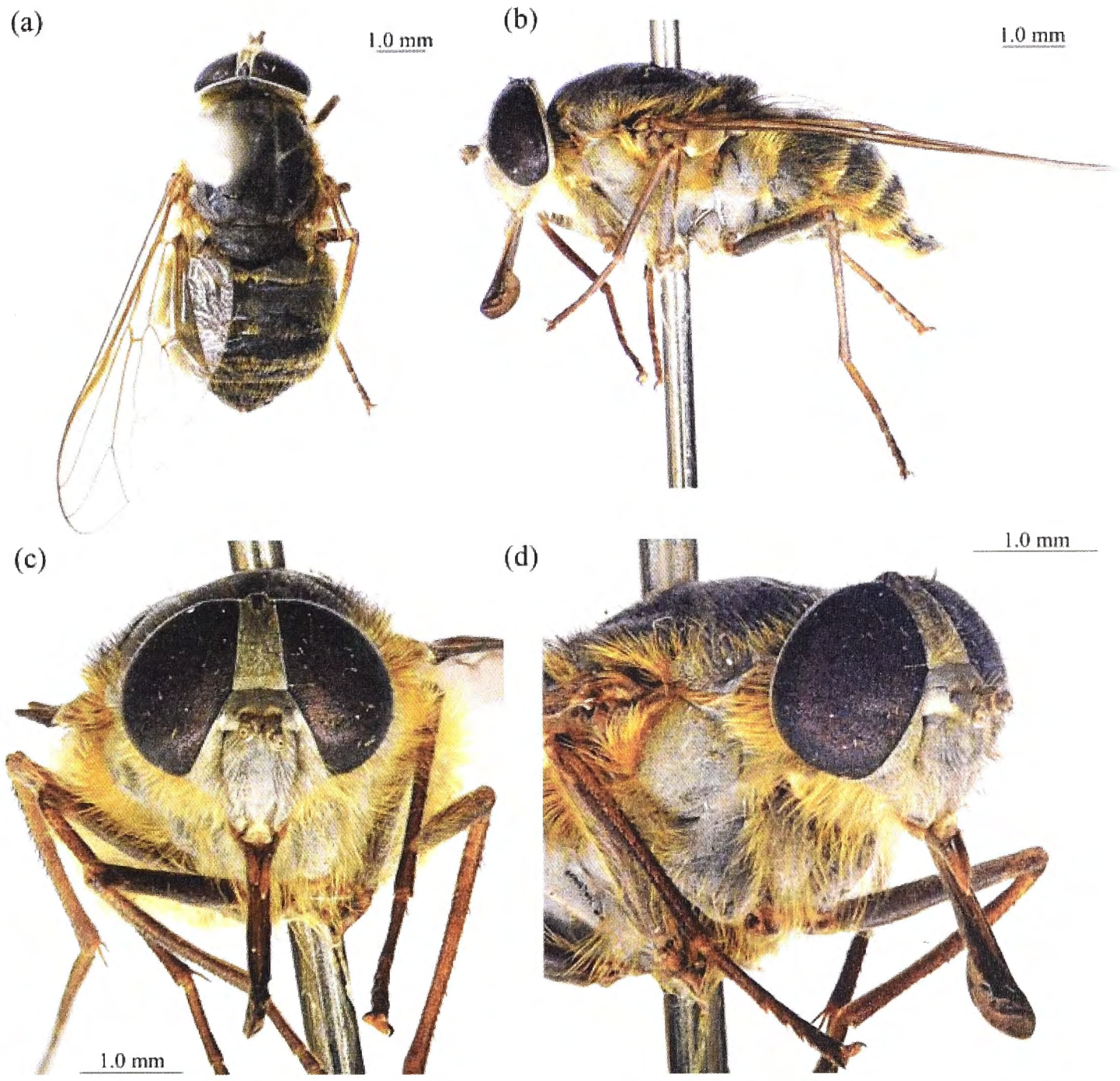

Fig. 2 *Anzomyia chrysomallis* Lessard, sp.n. Holotype ♀: (a) dorsum; (b) side; (c) front; (d) profile. This figure is published in colour in the online edition of this journal, which can be accessed *via* http://www.brill.nl/ise

without hairs; parafacials pale grey, hairs long, entirely dull golden yellow; face grey, hairs predominantly long, dark brown and with a small pale golden yellow tuft below each antennae, central area without hairs. Antennae: Scape and pedicel greyish-brown, hairs long, mixed brown and golden yellow; flagellum absent for description. Palpi: First segment golden yellowish brown with long, dull golden yellow hairs; second segment double the length of the first, somewhat blunt and relatively flat distally, brown, with an obvious bright golden to yellowish-brown elongated apical oval area that is bare, more yellowish on distal half, hairs predominantly golden yellow. Beard golden yellow. Thorax: Scutum and scutellum dark grey with a bluish hue, with indications of pale grey dorsocentral lines anteriorly and at sutures, and lighter grey anterior and lateral margins; disc hairs predominantly long and black, with some that are appressed golden yellow; notopleural hairs mixed black and golden yellow, relatively sparse;

supra- and postalar tufts mixed golden yellow with some sparse black medially; scutellar marginal hairs predominantly long black. Pleura pale to dark grey, with dense, entirely golden yellow hairs. Legs: Coxae grey with long golden yellow hairs, femora dark brown with grey tomentum and golden yellow hairs; tibiae and tarsomeres lighter brown, with predominantly short black hairs, fore legs with a dense golden brown ventral zone. Wings: Brownish-grey, somewhat yellowish along costal cell near base; stigma yellowish-brown, subtle; veins brown; R_4 angulate to slightly curved, without appendix; cell R_5 widely open. Abdomen: Dark greyish black with a bluish hue, not obviously banded, only the extreme edges of all tergites are marked with pale brown; hairs on disc a dull golden yellow, with a medial zone of black hairs on third and subsequent tergites, with dense golden yellow hairs on apical fringes and lateral margins. Venter: Dark greyish black, with pale brown bands on extreme distal edges of sternites, hairs on disc predominantly dense and golden brown.

Remarks

This specimen was originally determined by Ian Mackerras as "*Scaptia (Pseudoscione) anomala* var."

Distribution

This species is only known from the holotype, central-eastern NSW, Australia (Fig. 1).

Etymology

This specific epithet is derived from the Greek *chrysos*, gold, and *mallos,* wool, and refers to the distinct golden yellow hairs covering the species.

***Anzomyia pegasus* Lessard, sp.n.** (Fig. 3)

Type specimen

Holotype ♀, Australia, NSW, Kosciuszko National Park, 1.8 km NE of Thredbo, 36°29'49"S 148°18'51"E GPS, 1480 m, over narrow stream in flowering grassland, malaise, 11-13 Jan 2002, CL Lambkin and NT Starick (ANIC #29 005393). Paratype ♀ (1), Kosciuszko National Park, 3.2 km WSW of Thredbo, near Dead Horse Gap, 36°31'15"S 148°16'06"E GPS, 1496 m, over narrow stream in flowering grassland, malaise, 1-11 Jan 2002, CL Lambkin and NT Starick (ANIC #29 005392).

Diagnosis

A small (Length 10 mm) black species, superficially similar to *An. anomala*, but diagnosed as being darker, hairier, and with a more obviously projecting face, longer palpi over half the length of the proboscis shaft, and dark grey to black scutum with less pronounced vittae, with the scutum and abdomen having dense golden yellow hairs that sharply contrasts the darker ground colour.

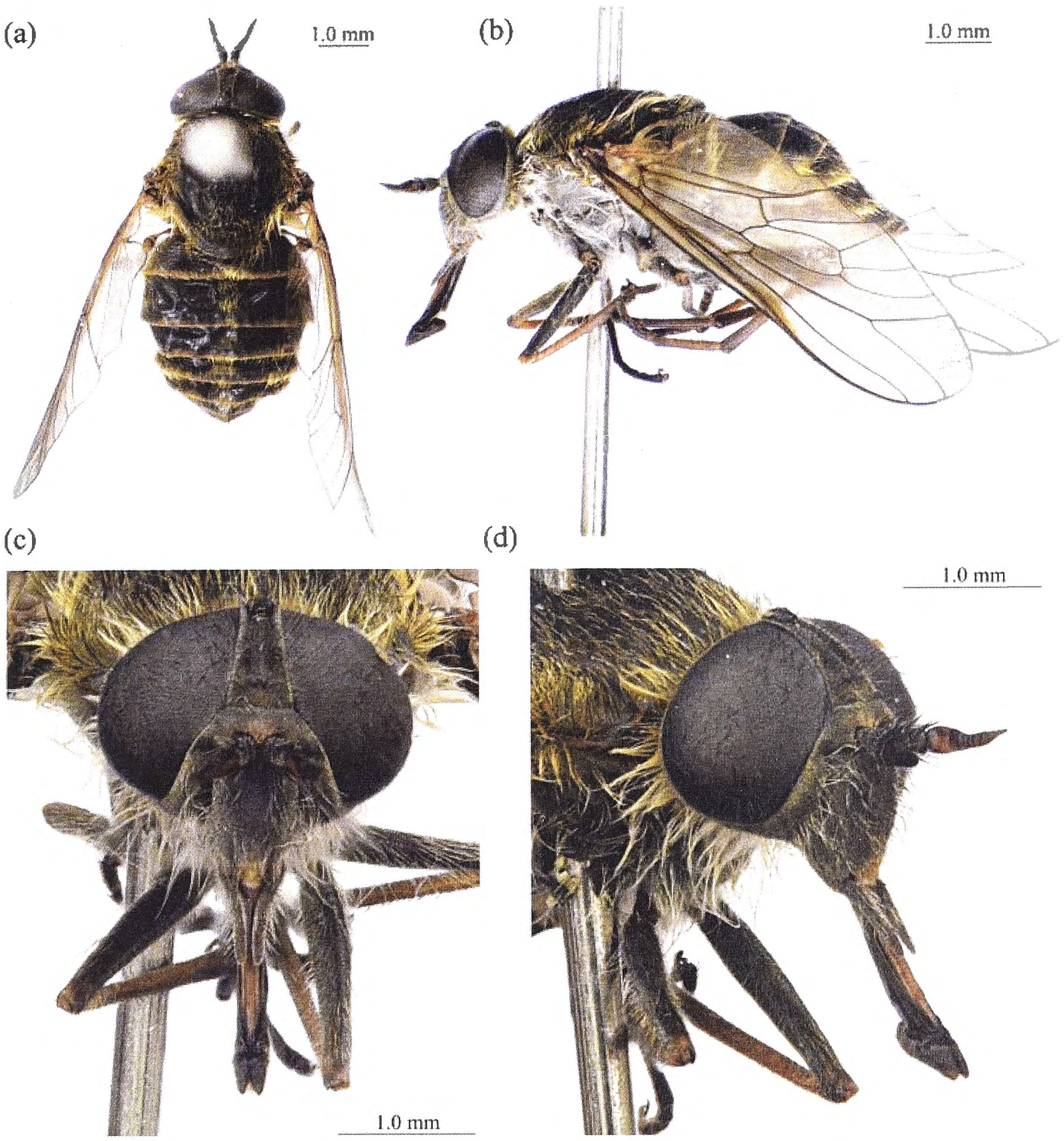

Fig. 3 *Anzomyia pegasus* Lessard, sp.n. Holotype ♀: (a) dorsum; (b) side; (c) front; (d) profile. This figure is published in colour in the online edition of this journal, which can be accessed *via* http://www.brill.nl/ise

Female. Length 10 mm. Head: Eyes with long dark brown hairs. Frons strongly diverging, index 2.5, dark blackish, pale grey along eye margins and fawnish brown at lower margins, hairs long, black, with a sparse white patch at lower margin near the subcallus; ocellar tubercle raised, dark brown with long dark brown hairs. Subcallus dark blackish grey, fawnish brown near base of antennae, without hairs; parafacials dark blackish grey with pale fawnish grey zone along eye margins, hairs long, black along lateral margins, pale creamy white at lower medial margins towards face; face dark blackish grey, hairs long, mixed black and pale creamy white below each antennae, bare at centre. Antennae: Scape and pedicel dark brown to black, with grey tomentum,

hairs long and black; flagellomeres relatively well defined, dark brown, becoming more yellowish brown ventrally on medial surface. Palpi: First segment dark brown to black with grey tomentum, hairs creamy white; second segment over half the length of the proboscis shaft, dark brown to black with grey tomentum, with flat, lighter brown apical ovals that are slightly elongated, hairs creamy white basally and dark brown apically. Beard creamy white. Thorax: Dark grey to black, with evanescent pale grey dorsocentral lines anteriorly and at sutures, pale grey at anterior and lateral margins of scutum and apical margins of scutellum; disc with appressed dense golden yellow hairs sharply contrasting dark ground colour, with long, erect black hairs, scutellar hairs long, predominantly pale golden yellow with fewer black hairs at centre; notopleural hairs mixed golden yellow and black; supra-alar tuft pale golden yellow occasionally mixed with black, postalar tuft entirely pale golden yellow. Pleura dark grey to black, hairs sparse, predominantly creamy white, more yellowish on upper posterior margin of anepisternum. Legs: Coxae grey with pale creamy white hairs; femora dark brown to black with pale creamy white hairs, somewhat yellowish on distal segments; tibiae and tarsomeres lighter brown, contrasting femora, hairs dark brown, fore legs with a lighter golden brown ventral zone. Wings: Brownish-grey, slightly yellowish along costal cell near base; stigma yellowish-brown, subtle; veins brown, R_4 slightly curved to angulate, without appendix; cell R_5 widely open. Abdomen: Dark grey to black, with rather obvious pale brown apical bands and greyish brown medial triangles on all tergites; disc hairs black, with golden yellow hairs on obvious medial zones, apical fringes, and lateral margins. Venter: Dark grey, with pale brown bands on apical quarter of all sternites, hairs predominantly pale creamy white.

Distribution

This species is limited to the type location of Kosciuszko National Park, southeastern Australia (Fig. 1). Furthermore, it appears to co-occur with *An. anomala.*

Etymology

This specific epithet is a latinised derivation of the winged horse Pegasos from Greek mythology, and refers to the projecting face of the species resembling the elongated nose of a horse.

***Anzomyia herculensis* Lessard, sp.n.** (Figs 4 and 5)

Type specimens

Holotype ♀, New Zealand, BR, Mt Hercules Scenic Reserve, Hercules Ck, yellow pan trap in podocarpl broadleaf forest, 1-3 Jan 1984, J.W. Early (ERM-LUNZ). Paratype ♀ (4), New Zealand, WD, Westland National Park, adjacent Canavans Knob, 140 m, malaise trap, 12-17 Jan 1982, J.W. Early (ERM-LUNZ). Paratype ♂ (1), same data as for Holotype (ERM-LUNZ). Paratype males (2), same data as for Paratype ♀ (ERM-LUNZ).

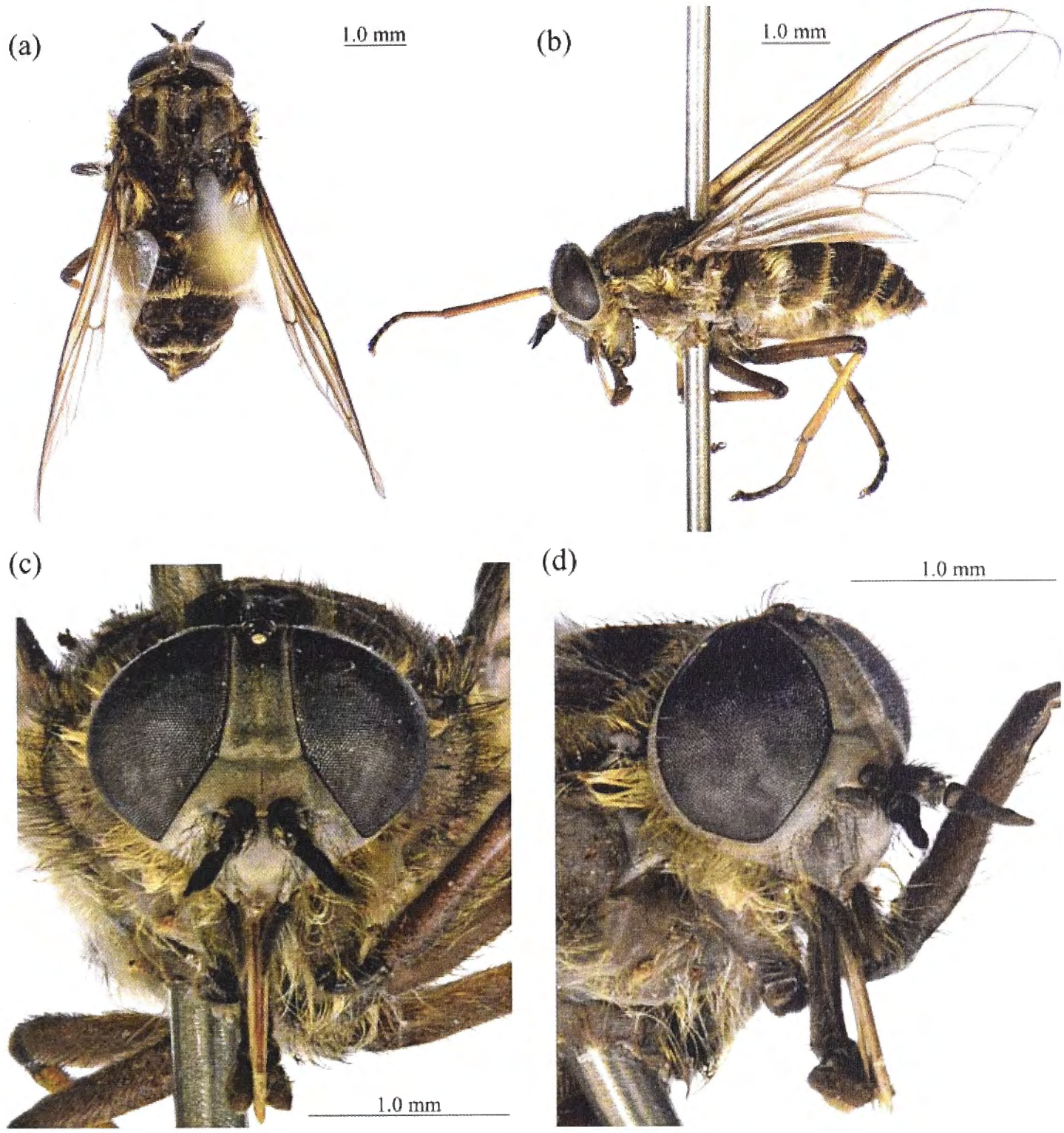

Fig. 4 *Anzomyia herculensis* Lessard, sp.n. Holotype ♀: (a) dorsum; (b) side; (c) front; (d) profile. This figure is published in colour in the online edition of this journal, which can be accessed *via* http://www.brill.nl/ise

Other specimens examined

♂ (3), New Zealand, BR, Paparoa Ranges, 2 km N of Croesus Knob, sweeping tussock, 1130 m, 20 Jan 1982, J.W. Early and R.M. Emberson (ERM-LUNZ). ♂ (1), New Zealand, BR, Punakaiki Scenic Reserve, Bullock Ck, 20 m, malaise trap, 24 Jan to 8 Feb 1983, G.R. Champness (ERM-LUNZ).

Diagnosis

A very small (length 6–10 mm), dark species, similar to *An. pegasus*, but separated by its short, relatively thick antennae, subcylindrical palpi, scutum with obvious grey

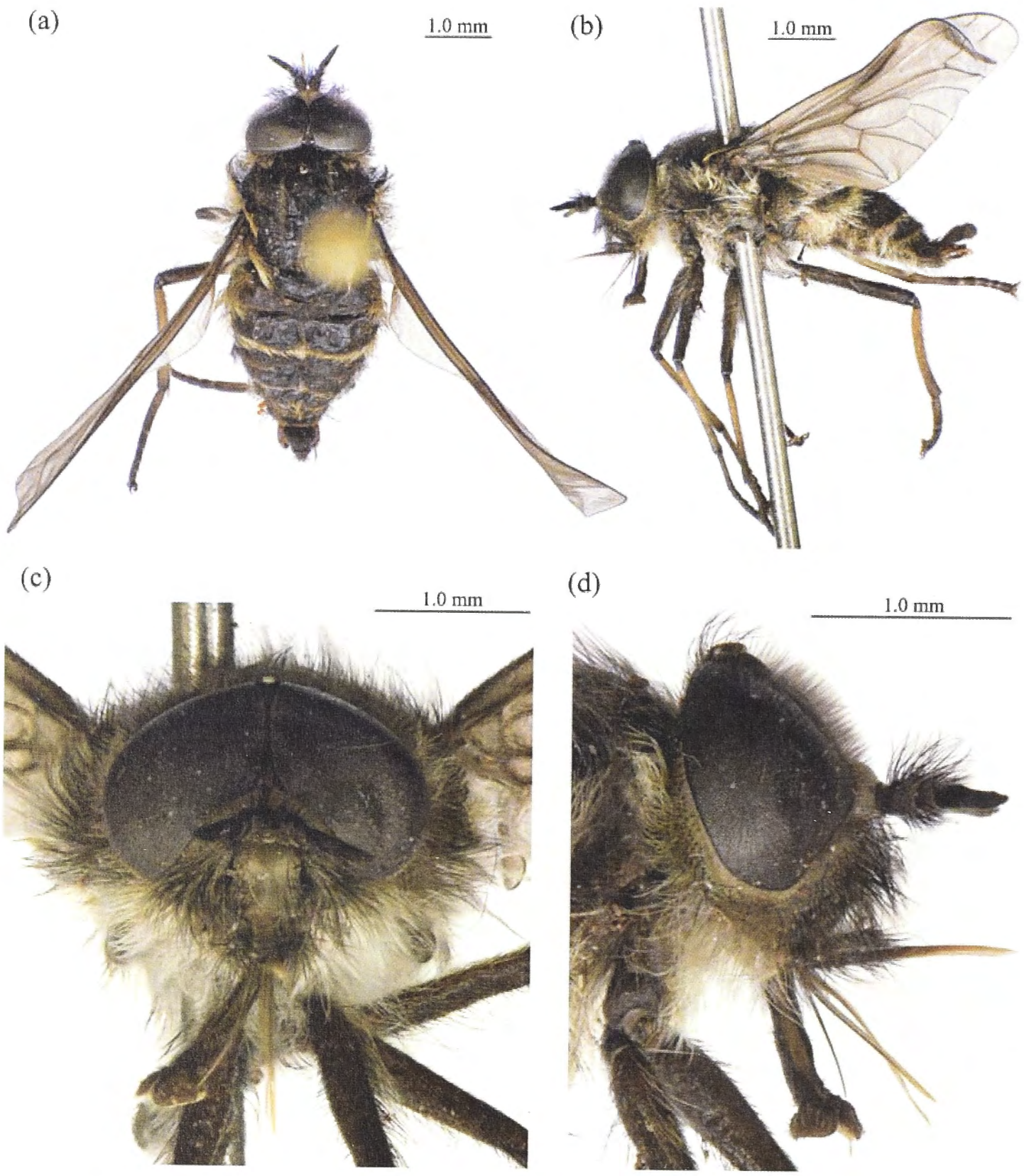

Fig. 5 *Anzomyia herculensis* Lessard, sp.n. Paratype ♂: (a) dorsum; (b) side; (c) front; (d) profile. This figure is published in colour in the online edition of this journal, which can be accessed *via* http://www.brill.nl/ise

postpronotal lobes contrasting dark ground colour, and well-defined grey vittae exceeding the suture, wings clouded, and with a relatively tapered abdomen with an apical fringe of black hairs on tergite three.

Female. Length 6–8 mm. Head: Eyes with relatively dense, long, dark brown hairs. Frons strongly diverging, index 2.2, with a slight sunken impression at base, greyish-brown, darker towards ocellar tubercle, hairs long dark brown; ocellar tubercle dark

brown, with long black hairs. Subcallus fawnish grey, without hairs; parafacials grey, hairs long, dark brown to black, with a yellowish cream tuft at lower margins; face grey, hairs long and black below antennae with some sparse pale yellow hairs, bare at centre. Antennae: Scape and pedicel dark brown to black with grey tomentum, hairs long, dense and black; flagellum relatively short and thick, dark brown to black with brown tomentum, flagellomeres not obviously defined. Palpi: First segment dark brown, with long, pale creamy yellow hairs; second segment three times larger than the first, subcylindrical, dark brown, with extremely reduced apical pits and short dense black hairs. Beard dull yellow to cream. Thorax: Scutum and scutellum dull, dark brown, with well defined grey medial and dorsocentral lines exceeding the suture, postpronotal lobe grey contrasting darker ground colour, lateral margins grey and less distinguished; disc mixed with long, erect black hairs and shorter appressed dull golden yellow ones, scutellum with long black hairs; notopleural hairs long, mixed black and dull golden yellow; supra- and postalar tufts rather dense, dull, and pale creamy gold. Pleura grey to dark brown, hairs predominantly pale creamy yellow, anepisternum with darker creamy yellow hairs dorsally and black at posteroventral margins. Legs: Coxae brownish grey, with mixed creamy white and pale yellow hairs above, with some black bellow; femora brown, pale yellowish brown on hind pair, knees black, hairs mixed with black and pale yellow; tibiae and tarsomeres pale creamy yellow to brown, contrasting darker femora, hairs short black, fore legs with a golden brown ventral zone. Wings: Brownish grey, moderately clouded, with yellowish brown along costal cell near base; stigma yellowish brown, subtle; veins brown; R_4 angulate to slightly curved, without appendix; cell R_5 widely open. Abdomen: Relatively tapered at end, dull, dark brown to black with subtle pale medial triangles, hairs on disc black, with dense pale creamy yellow hairs on medial triangles, apical fringes and marginal hairs black on tergite three and pale yellow to creamy white on remainder. Venter: Greyish brown, with occasional yellowish brown incursions, and narrow pale creamy apical bands, hairs creamy white.

Male. Length 6–10 mm. Similar to female but hairier. Eyes with upper facets not obviously enlarged. Palpi shorter, slender and more cylindrical than female, with a smaller yellow bare area distally. Beard rather creamy white. Hind femora dark brown to match fore and mid legs. Venter with additional black hairs on disc.

Remarks

The three male specimens from Paparoa Ranges are slightly larger (9–10 mm) and darker, but otherwise similar. We interpret this as intraspecific variation.

Distribution

Occurring in the central West Coast region of the South Island, New Zealand (Fig. 1).

Etymology

This specific epithet refers to the type locality.

Acknowledgements

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Chapter Five

Seven new species of the southern hemisphere horse fly subgenus *Scaptia* (*Pseudoscione*) (Diptera: Tabanidae), including descriptions and a revised key

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Chapter Five

MORPHOLOGY, SYSTEMATICS, EVOLUTION

Seven New Australian Species of the Southern Hemisphere Horse Fly Subgenus *Scaptia* (*Pseudoscione*) (Diptera: Tabanidae), Including Descriptions and a Revised Key

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J. Med. Entomol. 49(6): 1206–1225 (2012); DOI: http://dx.doi.org/10.1603/ME12028

ABSTRACT Horse flies (Diptera: Tabanidae) are ecologically important pollinators and vectors of many disease-causing organisms, as adult females are known to mechanically transfer multiple disease agents during feeding affecting humans, livestock, and many native mammals. *Scaptia* (*Pseudoscione*) Lutz in Lutz, Araujo, & Fonseca 1918 has the widest distribution of all genera in the tribe Scionini, occurring in Australia, New Guinea, New Zealand, and South America. Seven new species of Australian *S.* (*Pseudoscione*) are described and included in an updated key to the subgenus. The new species are: *S.* (*Pseudoscione*) *baylessi* sp. nov. Lessard, *S.* (*Pseudoscione*) *casseli* sp. nov. Lessard, *S.* (*Pseudoscione*) *mackerrasi* sp. nov. Lessard, *S.* (*Pseudoscione*) *moritae* sp. nov. Lessard, *S.* (*Pseudoscione*) *turcatelae* sp. nov. Lessard, *S.* (*Pseudoscione*) *turneri* sp. nov. Lessard, and *S.* (*Pseudoscione*) *wiegmanni* sp. nov. Lessard. In addition, *S.* (*Pseudoscione*) *occidentalis* Mackerras, 1960, previously described as a subspecies, has been raised to species level. One new species significantly extends the known distribution of *Scaptia* into central Australia, >1,200 km NW from the nearest recorded species within the subgenus.

KEY WORDS Pangoniinae, Scionini, *Copidapha*, morphology, taxonomy

Horse flies, commonly referred to as deer or march flies, are one of the most recognized groups of blood-feeding Brachycera, with over 4,400 extant species described throughout the world (Evenhuis et al. 2009). The family is sexually dimorphic in feeding habit as only females require a bloodmeal for ovary development, and consequently, can mechanically transmit diseases including anaplasmosis (Scoles et al. 2008) and bovine leukemia virus in cattle, equine infectious anemia in horses (Foil et al. 1984, 1988), and trypanosomiases and infections of thefi larial nematode *Pelecitus roemeri* in kangaroos (Spratt 1972a,b, 1974a,b, 1975; Reid et al. 2001). Human diseases are also spread through feeding, such as loiasis, tularaemia, and even anthrax (Krinsky 1976, Foil 1989). The Australian species *Scaptia* (*Pseudoscione*) *regisgeorgii* (Taylor) 1918, *Scaptia* (*Pseudoscione*) *xanthopilis* (Ferguson 1921), *Scaptia* (*Pseudoscione*) *concolor* (Walker 1850), and *Scaptia* (*Pseudoscione*) *neoconcolor* (Mackerras 1960) have been recorded to feed on humans, with the latter two also attacking horses (Mackerras 1960; unpublished data).

Interestingly, horse flies are also important pollinators (Johnson and Morita 2006, Morita 2008) as all males, and some females, feed exclusively on the nectar and pollen of plants; *Grevillea*, *Melaleuca*, and other Myrtaceae are all fed on by Australian Tabanidae (Mackerras 1960). The tea-tree genus *Leptospermum* is frequently visited by adults of *Scaptia* (*Pseudoscione*) *calabyi* Mackerras, 1960, and *Scaptia* (*Pseudoscione*) *vicina* (Taylor 1918) in Australia, with the former also collected from *Eucalyptus* (Mackerras 1960; unpublished data). New Zealand species also feed from *Leptospermum*, including *Scaptia* (*Pseudoscione*) *adrel* (Walker, 1850), *Scaptia* (*Pseudoscione*) *lerda* (Walker, 1850), and *Scaptia* (*Pseudoscione*) *milleri* Mackerras, 1957 (Tillyard 1926, Mackerras 1960; unpublished data). Commonly, many species are known to feed on both mammals and plants; the Australian species *Scaptia* (*Pseudoscione*) *maculiventris* (Westwood, 1835) and *Scaptia* (*Pseudoscione*) *subcontigua* (Ferguson 1921) feed from horses, humans and/or *Leptospermum* (Mackerras 1960), whereas the Chilean *Scaptia* (*Pseudoscione*) *viridiventris* (Macquart, 1838) is attracted to both humans and the plant genus *Luma* (Myrtaceae) (unpublished data).

The monophyly of the Tabanidae is well supported by both morphological (Mackerras 1954, Yeates 2002) and molecular evidence (Wiegmann et al. 2000, 2011; Morita 2008). However, species-level taxonomic work is impeded by the general morphological uniformity of both sexes in genitalia, especially below the tribal level (Mackerras 1954). Mackerras (1960) stated that "the male genitalia [give] no assistance in discriminating between species" for the genus *Scaptia* Walker 1850,

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and that large structural "differences in the genitalia bear little relation to degrees of difference in external characters" (Mackerras 1960, p. 36). Consequently, emphasis has been placed on coloration patterns and chaetotaxy, which can be modified over time because of fading or difference in specimen collection and curation (Mackerras et al. 2008; Morita 2008). Generally, these characters are still valid and used in delimiting species (Lessard and Yeates 2011, 2012).

Today, the classification of the Tabanidae is primarily based on the work of Mackerras (1954), who used external characters and available genitalia differences of adults. This scheme encompasses four subfamilies, with further division into their respective tribes: Chrysopsinae (Bouvieromyiini, Chrysopini, and Rhinomyzini), Pangoniinae (Mycteromyiini [added by Coscarón & Philip, 1979], Pangoniini, Philolichini, and Scionini), Scepsidinae, and the largest of the subfamilies, Tabaninae (Diachlorini, Haematopotini, and Tabanini).

The subfamily Pangoniinae comprises four tribes; the Mycteromyiini (Neotropical), Pangoniini (Australasian, Nearctic, Neotropical, and Palaeartic), Philolichini (Afrotropical, Australasian, and Oriental), and the Scionini (Australasian, Nearctic, and Neotropical) (Mackerras 1955). The Scionini is further divided into seven genera: *Anzomyia* Lessard 2012, *Caenopangonia* Krober 1930, *Fidena* Walker 1850, *Goniops* Aldrich 1892, *Pityocera* Giglio–Tos 1896, *Scione* Walker 1850, and the most species-rich genus, *Scaptia.*

Scaptia are usually stout and hairy flies, with a more slender proboscis than other Australian Tabanidae (Mackerras 1960). The genus has an exclusively southern hemisphere distribution, occurring predominantly in Australia and South America, with smaller assemblages in New Zealand and New Guinea (Coscarón and Wilkerson 1985, Coscarón and González 2001, Coscarón and Iide 2003, Daniels 1989, Lessard and Yeates 2011, in review; Mackerras 1957, 1960, 1961, 1964; Oldroyd 1947; Wilkerson and Coscarón 1984). Seven subgenera have been described and applied to *Scaptia*, including the more restricted *Lepmia* Fairchild 1969 (Brazil), *Pseudomelpia* Enderlein 1922 (Chile), *Myioscaptia* Mackerras 1955 (Australia), *Palimnecomyia* Taylor 1917 (Australia), and *Plinthina* Walker 1850 (Australia), compared with the more expansively dispersed and species-rich subgenera *Scaptia* Walker 1850 (Australia, Chile, Peru, Bolivia, and Argentina) and *Pseudoscione* Lutz in Lutz, Araujo, and Fonseca 1918 (Australia, Argentina, Brazil, Chile, New Guinea, and New Zealand).

Members of *Scaptia* (*Pseudoscione*) are medium to large, plump species with diverging frons, moderately projecting face, with relatively long slender proboscis and legs. *Scaptia* (*Pseudoscione*) is the most species-rich subgenus of *Scaptia*, with 66 extant species described today (including new spp. described herein and presented in Table 1). It is also the most widely distributed, occurring in Australia (32 spp., Table 1; Mackerras 1960), South America (16 spp.; Wilkerson and Coscarón 1984), New Guinea (11 spp.; Mackerras 1964, Oldroyd 1947), and New Zealand (six spp.; Mackerras 1957), and is the only representative of *Scaptia* in New Guinea and New Zealand.

Moreover, there appears to be three main, morphologically idiosyncratic assemblages of *S.* (*Pseudoscione*) pertaining to each continent (Fig. 1; Table 1); Australian and New Guinean species are considered morphologically analogous (Mackerras 1964) and can be identified by their wide and strongly diverging frons, faces that are moderately bulging to truncate with an obvious basal indentation, wider palpi, and a long proboscis at least one and a half times the length of the head height (Fig. 1A). Although originally described in *S.* (*Pseudoscione*) by Mackerras (1960), the exceptional species *Anzomyia anomala* (Mackerras 1960) was recently removed from *Scaptia* and raised to the Scionini genus *Anzomyia* Lessard, 2012 (Lessard and Yeates 2012). Nevertheless, New Zealand species are diagnosed as having large, slender, pointed, and dorsally rotated palpi, and a short, thick proboscis that is usually less than one and a quarter times the length of the head height, with a well developed, fleshy labella (Fig. 1B). Finally, South American members are distinguished from other *S.* (*Pseudoscione*) by their strongly projected faces with basal elongation, small, and slender palpi, and a slender proboscis with small labella (Fig. 1C), common to *Scione* and *Fidena,* also from South America (Mackerras 1955).

The taxonomy of Australian Tabanidae is quite mature, with a series of recent taxonomic articles being published renewing the descriptive work of the family (Mackerras et al. 2008; Lessard and Yeates 2011, 2012). New material has accumulated in Australian collections since Mackerras' 1960 revision of the genus, as we describe, name, and illustrate seven new species of *S.* (*Pseudoscione*), as well as modifying the existing key of Mackerras (1960) to include all known species. Additionally, *Scaptia* (*Pseudoscione*) *mackerrasi* Lessard, sp. nov. significantly extends the known distribution of *Scaptia* inland to central Australia by over 700 km from the nearest species record for the genus, suggesting that *Scaptia* is able to tolerate arid environments.

Materials and Methods

Morphological terminology follows Mackerras et al. (2008). Frons index was defined by Mackerras (1955) as the "length from vertex to top of subcallus, divided by width at mid-length of the frons" (Mackerras 1955, p. 459). Specimens were examined using Zeiss dissecting microscopes. Photographs were acquired on a BK Plus Lab System featuring a P-51 Cam lift, Infinity Optics K2 Long Distance Microscope, and Helicon Focus software. All material is sourced from the Australian National Insect Collection at Commonwealth Scientific and Industrial Research Organization Ecosystem Sciences, Canberra ACT, unless otherwise stated. Collection localities are displayed in Fig. 2.

A list of abbreviations is as follows: ANIC, Australian National Insect Collection, Commonwealth Scientific

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Table 1. Species list of the southern hemisphere horse fly subgenus *Scaptia* (*Pseudoscione*) Lutz in Lutz, Araujo, & Fonesca 1918, including the new species described herein (Mackerras 1957, 1960, 1964; Oldroyd 1947; Wilkerson and Coscarón 1984)

Continent	Recognized species		
Australia (n = 32)	The *clavata* group	(*Ps.*) *occidentalis* Mackerras, 1960	(*Ps.*) *moritae* Lessard sp. nov.
	(*Ps.*) *clavata* (Macquart, 1838)	(*Ps.*) *regisgeorgii* (Taylor, 1918)	(*Ps.*) *neoconcolor* Mackerras, 1960
	(*Ps.*) *orientalis* Mackerras, 1960	(*Ps.*) *rufonigra* (Ferguson, 1921)	(*Ps.*) *quadrimacula* (Walker, 1848)
	(*Ps.*) *gemina* (Walker, 1848)	(*Ps.*) *subappendiculata* (Macquart, 1850)	(*Ps.*) *roei* (Macleay, 1826)
		(*Ps.*) *subcontigua* (Ferguson, 1921)	(*Ps.*) *turcatelae* Lessard sp. nov.
	The *maculiventris* group	(*Ps.*) *testaceomaculata* (Macquart, 1850)	(*Ps.*) *turneri* Lessard sp. nov.
	The *maculiventris* subgroup	(*Ps.*) *xanthopilis* (Ferguson, 1921)	(*Ps.*) *wiegmanni* Lessard sp. nov.
	(*Ps.*) *auripleura* (Taylor, 1917)		
	(*Ps.*) *bicolorata* (Taylor, 1918)	The *concolor* subgroup	The *vicina* group
	(*Ps.*) *calabyi* Mackerras, 1960	(*Ps.*) *aureohirta* (Ricardo, 1900)	(*Ps.*) *vicina* (Taylor, 1918)
	(*Ps.*) *georgii* (Taylor, 1918)	(*Ps.*) *baylessi* Lessard sp. nov.	
	(*Ps.*) *guttipennis* (Ferguson, 1924)	(*Ps.*) *casseli* Lessard sp. nov.	Unplaced species
	(*Ps.*) *maculiventris* (Westwood, 1835)	(*Ps.*) *concolor* (Walker, 1850)	(*Ps.*) *ianthina* (White, 1915)
	(*Ps.*) *neotricolor* (Taylor, 1918)	(*Ps.*) *lasiophthalma* (Macquart, 1834)	(*Ps.*) *mackerrasi* Lessard sp. nov.
New Guinea (n = 11)	The *maculiventris* group:	The *concolor* subgroup	(*Ps.*) *floccosa* Oldroyd, 1947
	The *maculiventris* subgroup	(*Ps.*) *auripilosa* Oldroyd, 1947	(*Ps.*) *insularis* Oldroyd, 1947
	(*Ps.*) *albibarba (Schuurmans* Stekhoven, 1926)	(*Ps.*) *bernhardi* Oldroyd, 1947	(*Ps.*) *leonina* Oldroyd, 1947
		(*Ps.*) *caliginosa* (Walker, 1865)	(*Ps.*) *novaeguineensis* (Ricardo, 1913)
	(*Ps.*) *unilineata* Oldroyd, 1947	(*Ps.*) *flavibarbis* Oldroyd, 1949	(*Ps.*) *taylori* Oldroyd, 1947
New Zealand (n = 6)	The *adrel* group	(*Ps.*) *lerda* (Walker, 1850)	The *montana* group
	(*Ps.*) *adrel* (Walker, 1850)	(*Ps.*) *milleri* Mackerras, 1957	(*Ps.*) *montana* (Hutton, 1901)
	(*Ps.*) *brevipalpis* Kröber, 1931	(*Ps.*) *ricardoae* (Hutton, 1892)	
South America (n = 16)	(*Ps.*) *albifrons* (Macquart, 1838)	(*Ps.*) *grisea* (Jaennicke, 1867)	(*Ps.*) *subandina* (Philippi, 1865)
	(*Ps.*) *atra* (Philippi, 1865)	(*Ps.*) *hibernus* Wilkerson & Coscarón, 1984	(*Ps.*) *subulipalpis* Enderlein, 1929
	(*Ps.*) *australis* (Philippi, 1865)	(*Ps.*) *latipalpis* (Macquart, 1849)	(*Ps.*) *viridiventris* (Macquart, 1838)
	(*Ps.*) *dorsoguttata* (Macquart, 1850)	(*Ps.*) *leucothorax* (Ricardo, 1900)	(*Ps.*) *vittata* (Philippi, 1865)
	(*Ps.*) *fenestrate* (Macquart, 1846)	(*Ps.*) *longipennis* (Ricardo, 1902)*	
	(*Ps.*) *flavipes* (Enderlein, 1929)	(*Ps.*) *stictica* Wilkerson & Coscarón, 1984	

The species *Anzomyia anomala* (Mackerras 1960) was recently removed from *S.* (*Pseudoscione*) and placed in the Scionini genus *Anzomyia* Lessard 2012 (Lessard and Yeates 2012). Asterisk indicates type species.

and Industrial Research Organization Ecosystem Sciences, Canberra, Australia; GDCB, Greg Daniels Private Collection, Brisbane, Queensland, Australia; NSW, New South Wales; NT, Northern Territory, Qld Queensland; QDPI, Queensland Department of Primary Industries, Indooroopilly, Australia; QM, Queensland Museum, Brisbane, Australia; SA, South Australia; SAM, South Australian Museum, Adelaide, Australia; UQIC, University of Queensland Insect Collection, Brisbane, Australia.

Results

Taxonomy

Subgenus PSEUDOSCIONE Lutz in Lutz, Araujo, and Fonseca, 1918.

Clanis Walker, 1850, p. 9, misapplied name of Hübner, 1816 (Lepidoptera). Type species *Pangonia contigua* Walker, 1848 (=*Pangonia lasiophthalma* Macquart, 1834), Australia, by designation of Coquillett 1910, p. 524.

Pseudoscione Lutz in Lutz, Araujo, and Fonseca, 1918, p. 167. Type species *Diatomineura longipennis* Ricardo, 1902, Brazil, by designation of Fairchild 1950, p. 124.

Copidapha Enderlein, 1922, p. 337, 1925, p. 270. Monotypic for *Copidapha bifasciata* Enderlein, 1925 (=*Pangonia roei* Macleay, 1826), Australia. Synonymy by Ferguson 1926a, p. 303. Available if the Australian members are distinguished from the other continental fauna.

Scaptiella Enderlein, 1923, p. 544. Monotypic for *Pangonia aperta* Loew, 1859, "Lusitania," erroneous (=*Pangonia subappendiculata* Macquart, 1850, Australia).

Astypia Enderlein, 1925, p. 297. Type species *Pangonia jacksonii* Enderlein, 1925, misapplied name of Macquart, 1838 (=*Scaptia* (*Pseudoscione*) *calabyi*), Western Australia, by original description.

Lilaea Enderlein, 1922, p. 341, 1925, p. 297, misapplied name of Walker, 1850, by incorrect selection of *Pangonia roei* Enderlein, 1922; misapplied name of Macleay, 1826 (=*concolor* Walker, 1850), Australia as type species. Error corrected by Ferguson 1926a, p. 294, 304.

Scaptia (*Pseudoscione*) (Lutz in Lutz, Araujo, and Fonseca, 1918); Mackerras, 1955, p. 493, 1957, p. 586, 1960, p. 81, 1964, p. 79; Wilkerson and Coscarón, 1984, p. 213.

Diagnosis. The following subgeneric diagnosis for *S.* (*Pseudoscione*) was provided by Mackerras (1960, p. 83): "Female. Mostly medium-sized to rather large (range, 9–16 mm), plump species, with relatively long legs [Figs. 3–10]. Frons clearly diverging: Face mod-

Fig. 1. Head comparisons of the Australian, New Zealand, and South America members of the southern hemisphere subgenus *Scaptia* (*Pseudoscione*) Lutz in Lutz, Araujo, and Fonseca (1918). (A) *Scaptia* (*Pseudoscione*) *roei* (Macleay, 1826), Australia. (B) *Scaptia* (*Pseudoscione*) *adrel* (Walker, 1850), New Zealand. (C) *Scaptia* (*Pseudoscione*) *longipennis* (Ricardo, 1902), Brazil. Scale bar, 1 mm. (Onlinefi gure in color.)

erately projecting. Proboscis long and slender, from one and a half to twice the head height, with relatively small, labellafi rm. Palpi less than half the length of the shaft; usually thick, pointed, and with a well-defined lateral bare area or concavity; occasionally truncate or slender. Wings never marbled, usually with at least a darker cloud across apices of basal cells; cell R_5 often narrowed or closed; cell M_3 always open; vein R_4 usually without appendix. Eighth sternite with gonopophyses usually triangular and approximated apically; cerci often truncate apically; lateral arms of furca not fused with ninth tergite (figs. 124–147, Mackerras 1960, p. 88, 98, 119). Male. Palpi sometimes slightly longer than in females, stout, cylindrical, exceptionally tapering to tip, with a small, subapical, dorsolateral bare concavity [Figs. 6 and 10]. Style of hypopygiumfi nger-like, rounded at tip (figs. 39–41, p. 33)."

Key to Females of Australian Species of *Scaptia* (*Pseudoscione*)

1. Face obviously protuberant or strongly bulging, without strong basal indentation (Fig. 11); scutal vittae strong; wings usually with stigma; Tasmania or central Australia 2

   Face truncated, somewhat indented at base (Figs. 3–10); scutal vittae absent or subtle; wings usually without obvious stigma; coastal mainland Australia 3

2. A large species (length 14 mm); frons almost parallel; palpi long and cylindrical, with flattened area rotated to point upward; wings with less obvious stigma; abdomen wide and flattened; Tasmania . . . . . *ianthina* (White 1915)

   A smaller species (length 9–11 mm); frons strongly diverging (Fig. 11); palpi relatively short, thick, and pointed, with deeply excavated lateral concavity; wings with strong stigma; abdomen short and rotund; central Australia . . . . . *mackerrasi* Lessard, sp. nov.

3. Palpi very slender, pointed with narrow bare concavity (fig. 102; Mackerras 1960); a large brown species (length 14–17 mm); scutum with well-defined yellowish brown vittae . . . . . *vicina* (Taylor 1918)

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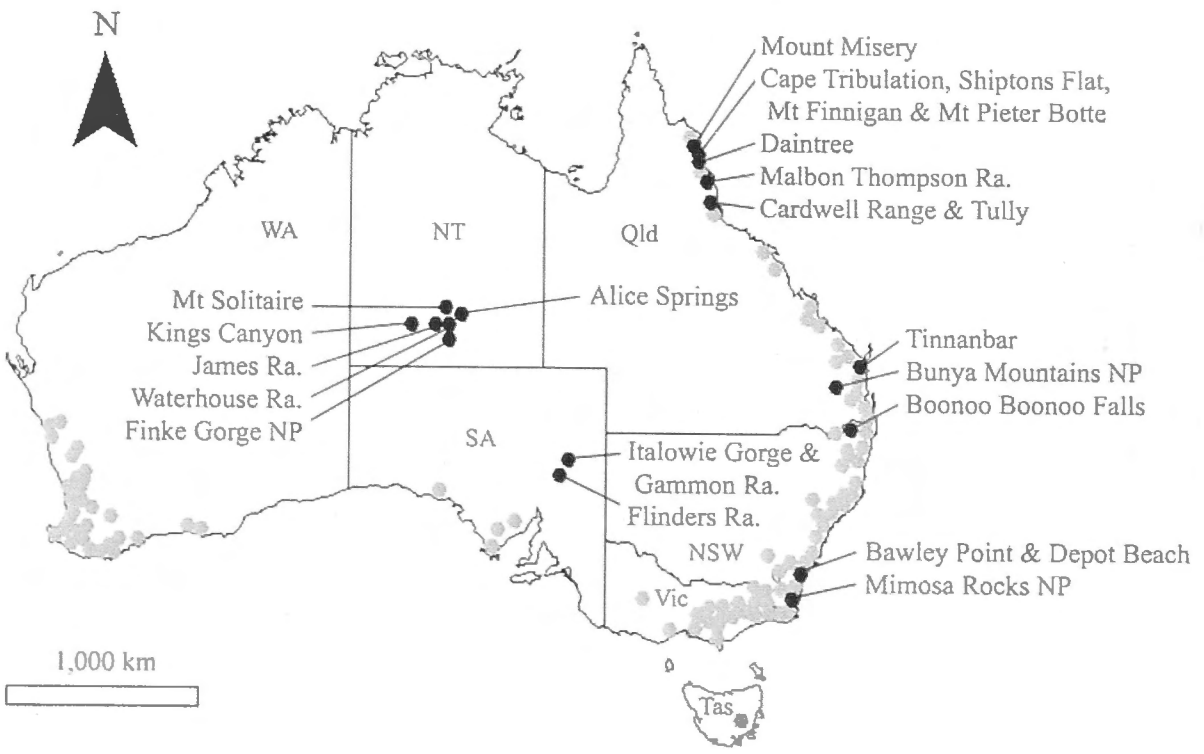

Fig. 2. Collection localities for the new Australian species of *Scaptia* (*Pseudoscione*) Lutz in Lutz, Araujo, and Fonseca 1918 described in this article, including thefi rst records of *Scaptia* from central Australia. Black represents collection records for the new species; gray represents previous collection records for the subgenus. NSW, New South Wales; NT, Northern Territory; Qld, Queensland; SA, South Australia; Tas, Tasmania; Vic, Victoria; WA, Western Australia; NP, National Park; Ra., Ranges.

Palpi not so slender with wide bare concavity (Figs. 3–10;fi gs. 99–101, 103–119); scutal vittae less pronounced or absent 4

4. Terminal segments of abdomen cylindrical (sometimes not apparent if retracted); large (13–15 mm) dark species, with black, scutal vittae gray; wings gray, often with darker markings on transverse veins; palpi very short 5

Terminal segments of abdomen dorsoventrally compressed; lighter species; palpi usually longer and more tapering 7

5. Wings uniformly gray; abdomen black, with median patches of white hair on tergites and dense white hairs on lateral margins . . . . . *clavata* (Macquart, 1838)

Wings less uniformly gray, usually with narrow darker markings at apices of basal cells, fork of R_{4+5} and apex of discal cell; abdomen usually predominantly brown, or with apical fringes of pale hairs on tergites 6

6. Palpi short and blunt (fig. 101); abdominal marginal hairs greyish white and black; genitalia as infi g. 125. Eastern Australia . . . . . *orientalis* Mackerras, 1960

Palpi narrower and tapering (fig. 100); abdominal marginal hairs almost completely white; genitalia as infi g. 126. Western Australia. . . . . *gemina* (Walker, 1848)

7. Antennal scape swollen, flagellum distinctly narrower than scape (fig. 104); palpi swollen; a small (9–12 mm), brown, tomentose species with clear or faintly stained wings. Western Australia . . . . . *regisgeorgii* (Taylor 1918)

Antennal scape normal, if at all, wider than flagellum; palpi less swollen 8

8. Palpi distinctly swollen (fig. 105); wings darkened anteriorly, with a clear spot at apex of *sc*, a broad dark band at apices of basal cells, and conspicuous dark spots at fork of R_{4+5} and apex of discal cell (plate 4,fi g. 33); a medium sized (11–12 mm), brown tomentose species, with well-defined, gray scutal vittae. Western Australia . . . . . *neotricolor* (Taylor 1918)

Palpi not swollen; wing markings not as above; scutal vittae usually not so prominent 9

9. Palpi slender, with flattened bare area (fig. 103); wings faintly yellow, without definite brown clouds or pattern . . . . . *subappendiculata* (Macquart, 1850)

Palpi stouter, either large (Figs. 5 and 8;figs. 116–119) or excavated laterally (Figs. 3, 4, and 7–9;fi gs. 104–112); wings mostly with definite clouds or bands (Figs. 3, 4, and 7), sometimes subtle (Figs. 5, 6, and 8–10) 10

10. Wings with a darker cloud (sometimes faint or narrow) at apices of basal cells, with or without additional faint spots or markings, and sometimes with the area beyond the discal cell gray (plate 1,fi g. 6; plate 4,fi g. 34); palpi usually less than one third the length of the proboscis shaft; scutum usually perceptibly vittate; abdomen generally with a pattern of black pigment and pale hairs 11

Wings with two dark bands (Figs. 3, 4, and 7), one at apices of basal cells, the other (occasionally rather vague: Figs. 5–6 and 9–10) extending to apex of discal cell, beyond which the wing is often distinctly gray; palpi equal to or more than one third the length of the proboscis shaft; scutum without evident paler vittae or dorsocentral sutural spots; abdominal markings indefinite 22

11. Wings somewhat yellowish anteriorly, with faint or evanescent band at apices of basal

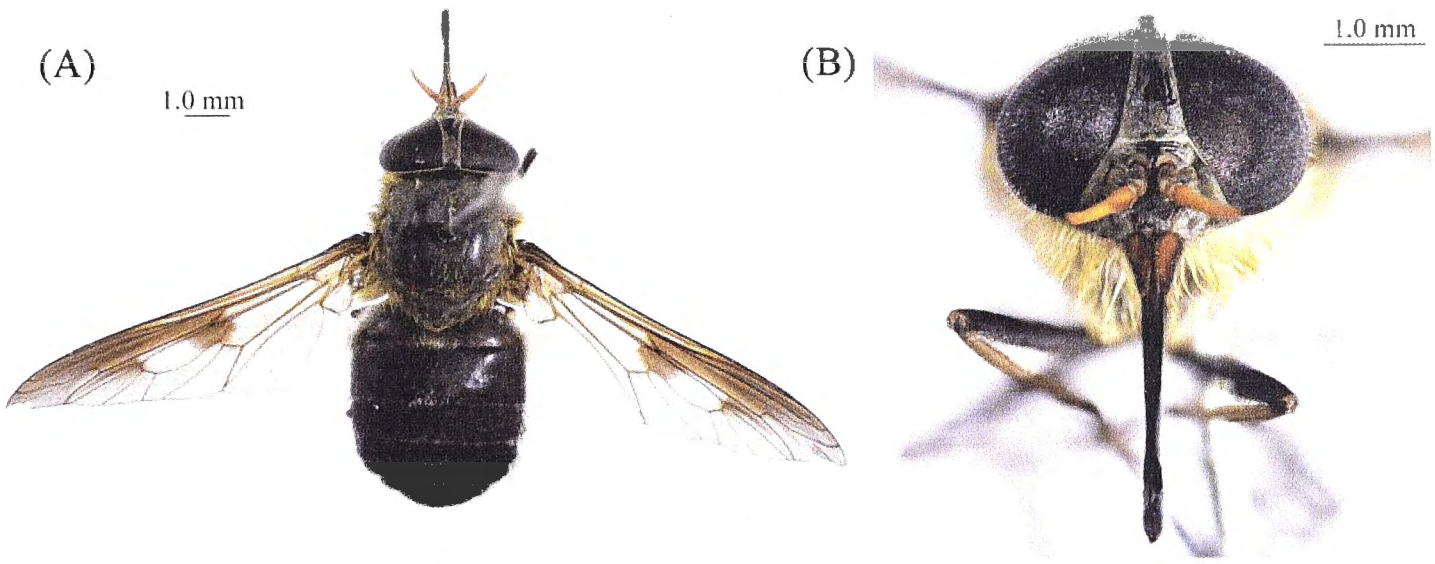

Fig. 3. *Scaptia* (*Pseudoscione*) *baylessi* Lessard, sp. nov. Holotype female. (A) Dorsum. (B) Front. (C) Side. (D) Profile. (Onlinefi gure in color.)

cells; abdomen patterns rather vague; beard and pleural hairs bright yellow 12

Wings more greyish, with better defined darker markings; abdominal patterns more definite; beard and pleural hairs usually cream to whitish 13

12. Palpi relatively broad (fig. 122); a robust (12–15 mm) species; scutum blackish gray, with a fringe of fawn; anterior half of abdomen red-brown with a median black vitta, posterior half all black, hairs creamy gold. Eastern Australia . . . . . *xanthopilis* (Ferguson 1921)

Palpi relatively narrow (fig. 111); a smaller (12–13 mm) species; scutum rather densely covered with golden hairs; abdomen light brown, somewhat darker apically, with a median black spot on second tergite, and bright golden hairs. Western Australia . . . . . *calabyi* Mackerras, 1960

13. Pale scutal vittae relatively well defined; palpi dark brown or greyish; femora entirely black or gray 14

At most indications of pale dorsocentral lines on scutum (Figs. 3–10); palpi reddish brown; femora at least partly yellow or reddish brown 16

14. Palpi more normal (fig. 108); wings without darker markings at fork of R_{4+5} and apex of discal cell; a robust species; eighth sternite as in fig. 131. New South Wales and Victoria . . . . . *testaceomaculata* (Macquart, 1850)

Palpi often rather club-shaped (fig. 106); wings with distinct darker spots at fork of R_{4+5} and apex of discal cell; a more slender species; eighth sternite as infi gs. 132 and 133. South and Western Australia 15

15. Beard and upper pleural hairs mostly yellow; apical four flagellomeres of antennae blackish brown, sharply contrasting . . . . . *occidentalis* Mackerras, 1960.

Beard and upper pleural hairs cream; apical flagellomeres of antennae diffusely darkened . . . . . *guttipennis* (Ferguson 1924)

16. Ground color of basal abdominal tergites dull, yellowish brown, occasionally entirely dark . . . 17

Ground color of basal abdominal tergites shining, rich red-brown 20

17. Femora entirely yellowish to reddish brown, occasionally with a black streak basally; large or small species 18

Femora black or gray on basal forth or more; relatively small species (10–12 mm) 19

18. A large species (14–15 mm); cloud at apices of basal cells diffuse; hairs on apical edges of abdominal tergites golden. Eastern Australia. . . . . *maculiventris* (Westwood, 1835)

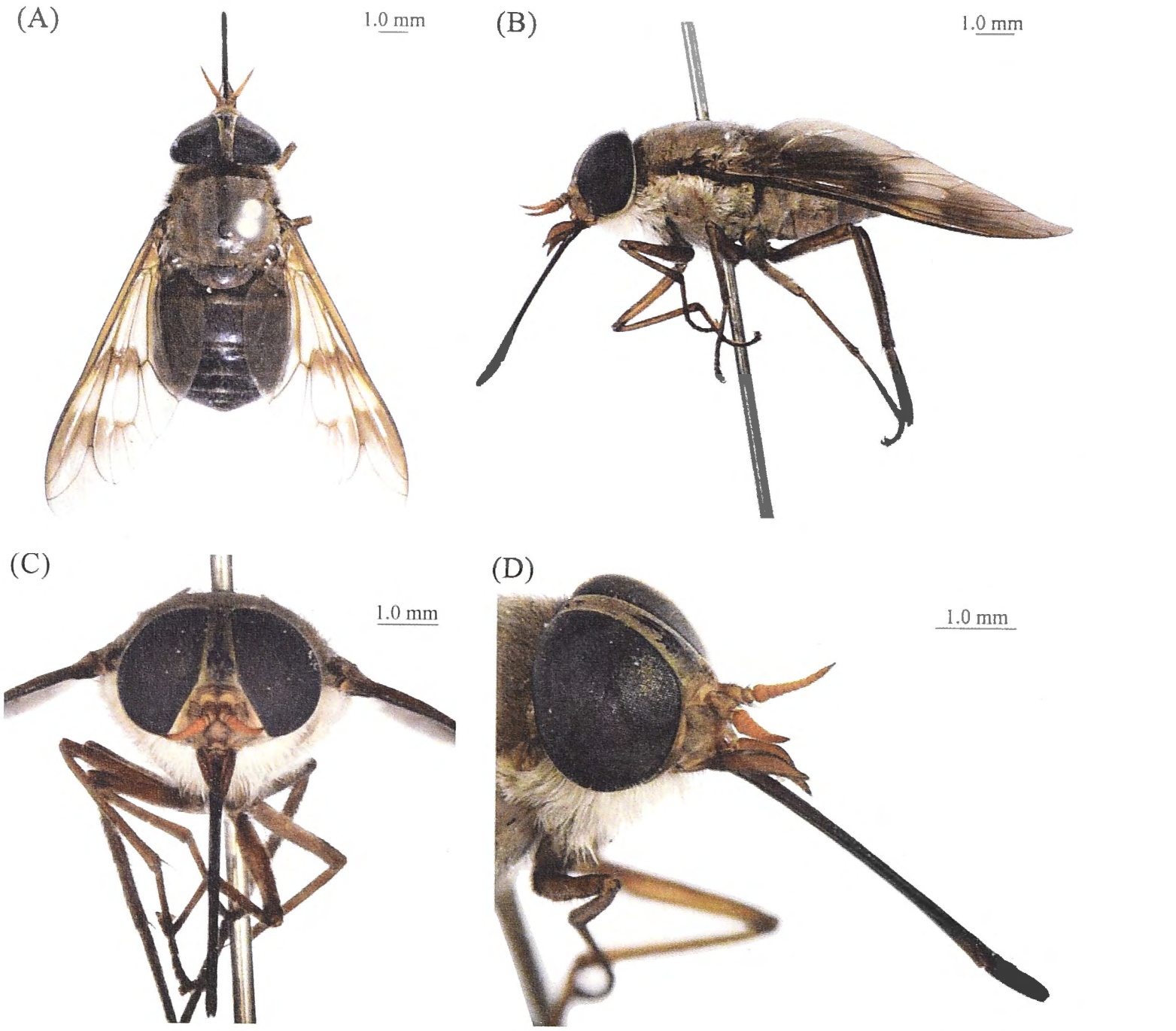

Fig. 4. *Scaptia* (*Pseudoscione*) *casseli* Lessard, sp. nov. Holotype female. (A) Dorsum. (B) Side. (C) Front. (D) Profile. (Onlinefi gure in color.)

A small species (9–12 mm); cloud at apices of basal cells dark, distinct; hairs on apical edges of abdominal tergites cream to yellowish cream. Western Australia . . . . . *bicolorata* (Taylor 1918)

19. Upper zone of pleural hairs yellow; lateral and segmental abdominal hairs bright golden; eighth sternite as infi g. 135; Eastern Australia. . . . . *auripleura* (Taylor 1917)

Pleural and lateral abdominal hairs cream, sometimes tinged with pale yellow; segmental abdominal hairs usually dark, except near median line; eighth sternite as infi g. 136. Western Australia . . . . . *georgii* (Taylor 1918) variety.

20. Proboscis more than twice the height of the head; palpi as in *maculiventris*; femora black on basal third only. Western Australia . . . . . *georgii* (Taylor 1918)

Proboscis about one and a half times the height of the head; palpi and femora otherwise. Eastern Australia 21

21. A smaller (12–13 mm) species, with shorter, wider palpi (fig. 113), and wider, black abdominal vitta; femora entirely red-brown . . . . . *rufonigra* (Ferguson 1921)

A larger (14–16 mm) species, with longer, narrower palpi (fig. 114), and narrower, black abdominal vitta; femora predominantly black . . . . . *subcontigua* (Ferguson 1921)

22. Marginal dense hairs on abdominal tergites mostly golden; scutum and scutellum not obviously contrasting, somewhat shiny 23

Marginal dense hairs on abdomen mostly pale on first and second tergites, mostly black on third and fourth, and with a rather conspicuous, posterolateral white tuft onfi fth or sixth 26

23. Scutum and abdomen deep brown; beard and thoracic hairs golden; legs deep brown to black; a large (14–15 mm) species; eyes bare. North Queensland . . . . . *roei* (Macleay, 1826)

Scutum lighter brown; abdomen yellowish brown; beard and thoracic hairs cream; legs yellowish brown; eyes hairy 24

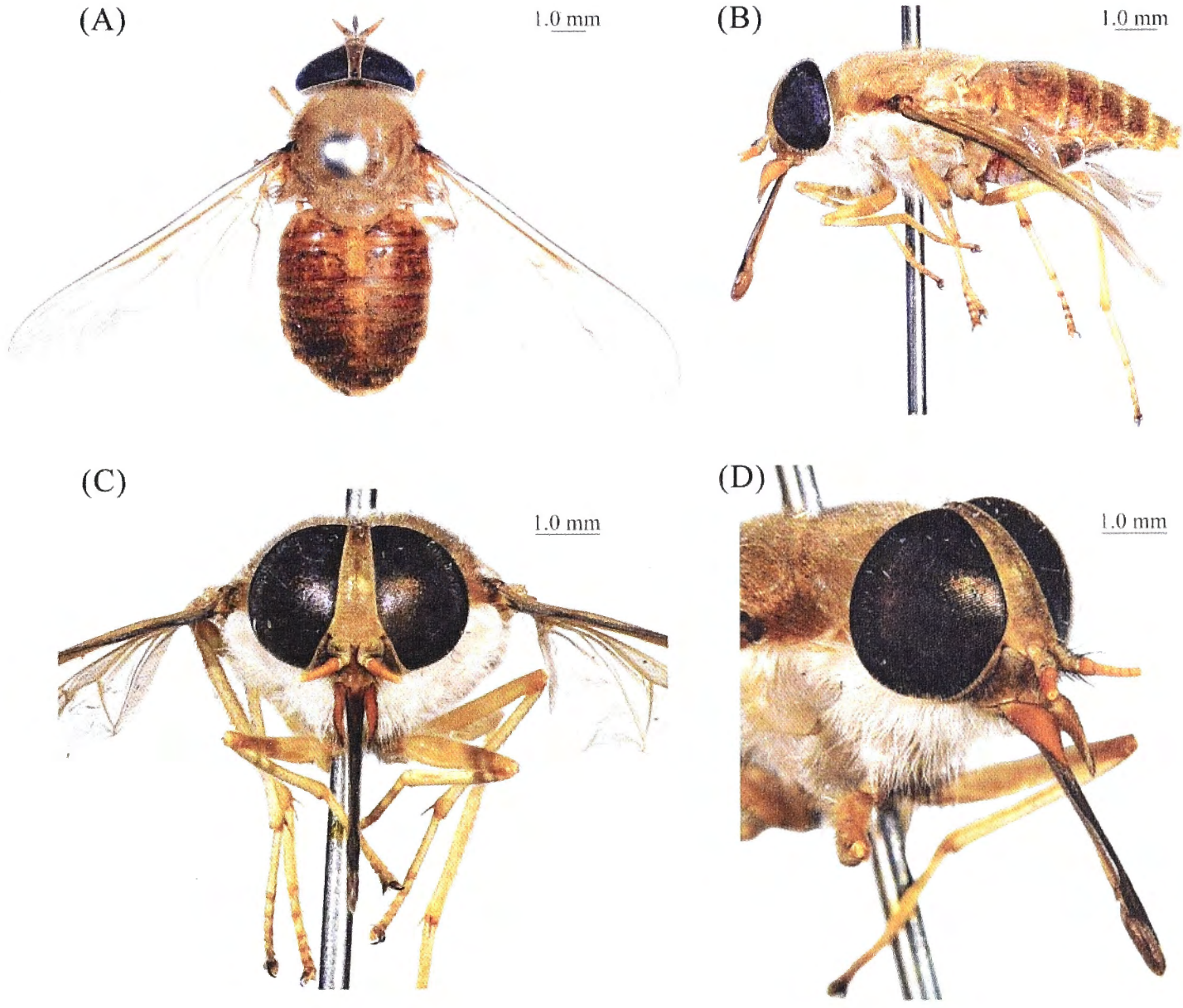

Fig. 5. *Scaptia* (*Pseudoscione*) *moritae* Lessard, sp. nov. Holotype female. (A) Dorsum. (B) Side. (C) Front. (D) Profile. (Onlinefi gure in color.)

24. Palpi wide, with slightly raised dorsal ridge (Fig. 5); scutum light greyish brown, hairy, contrasting with smoother, darker brown abdomen; abdomen with distinct pale medial stripe on all tergites (Figs. 5 and 6) . . . . . *moritae* Lessard, sp. nov.

    Palpi more slender and curved (fig. 117); scutum and abdomen more concolorous; abdomen uniform, often darker apically, without medial stripe 25

25. Smaller (12–13 mm) species; scutum violet-brown; abdomen and legs darkened on apical segments; beard and pleural hairs creamy yellow. North Queensland . . . . . *neoconcolor* Mackerras, 1960

    Larger (13–15 mm) species; scutum, abdomen and legs almost concolorous dull brown; beard and pleural hairs creamy white. South Queensland and New South Wales . . . . . *concolor* (Walker, 1850)

26. Smaller species (length 10–12 mm); scutum without obvious vittae (Figs. 3, 4, and 7); abdomen dull, not obviously shining 27

    Larger more robust species (length 13–16 mm); scutum with indications of vittae (Figs. 9 and 10); abdomen shining 30

27. Beard and pleural hairs creamy white; scutum greyish brown, with faint vittae; femora brown 28

    Beard and pleural hairs creamy yellow; scutum greyish black, without vittae; femora dark blackish brown 29

28. Scutum dark greyish brown (Fig. 7); wing pattern on discal cell evanescent, weaker than basal cells; abdomen shining, with anterior golden brown tergites contrasting to those darker brown posteriorly . . . . . *turcatelae* Lessard, sp. nov.

    Scutum pale greyish brown (Fig. 4); wing pattern on discal cell obvious, equal in intensity to basal cells; abdomen dull, concolorous dark brown . . . . . *casseli* Lessard, sp. nov.

29. Antennae bright yellowish brown; pleural hairs entirely creamy yellow (Fig. 3); bifusciate wing pattern obvious . . . . . *baylessi* Lessard, sp. nov.

    Antennae and palpi dull brown; posterior third of pleura and upper anepisternum with creamy white hairs (Fig. 8); wing pattern reduced to a single marking on apices of basal cells . . . . . *turneri* Lessard, sp. nov.

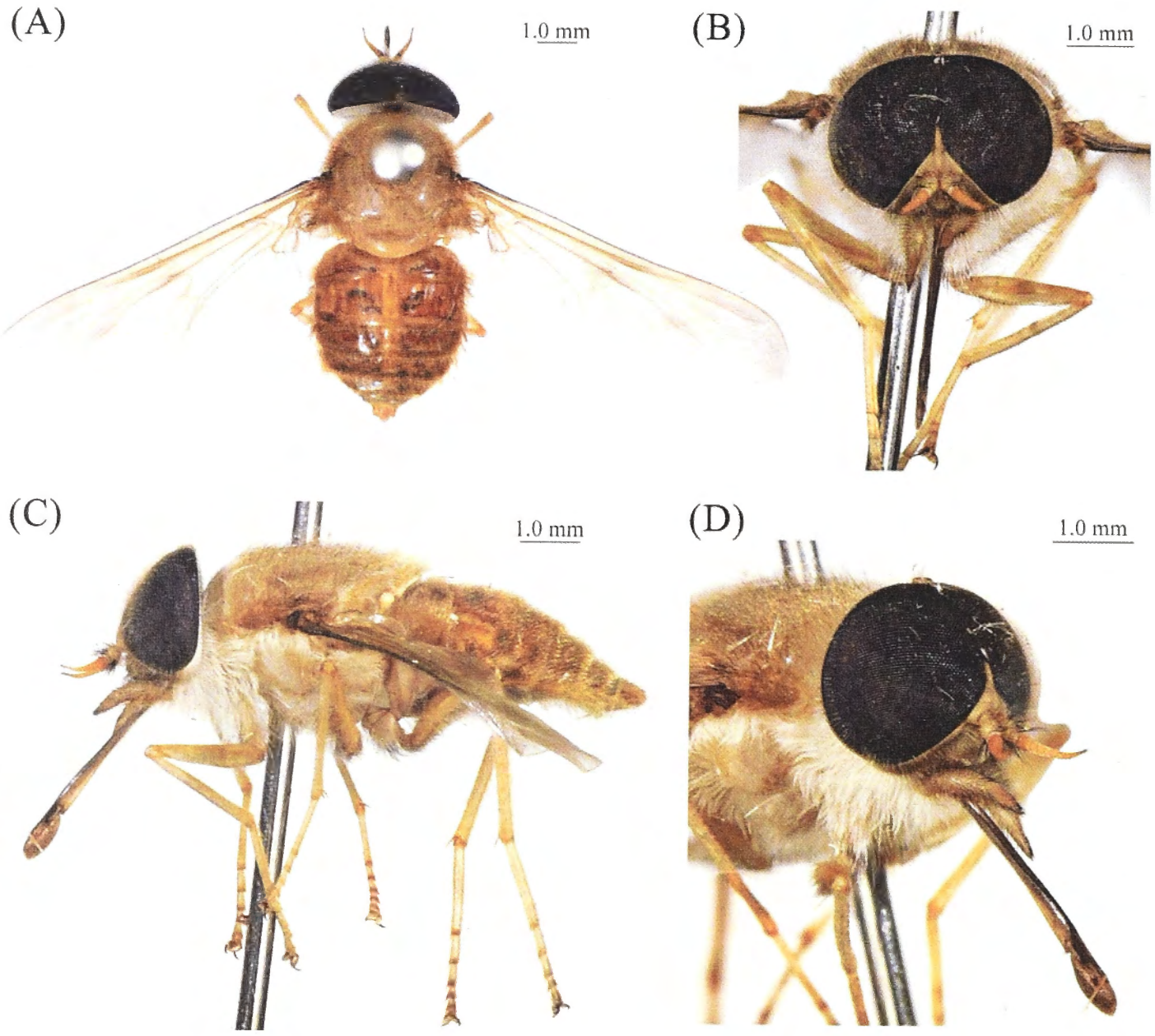

Fig. 6. *Scaptia* (*Pseudoscione*) *moritae* Lessard, sp. nov. Paratype male. (A) Dorsum. (B) Front. (C) Side. (D) Profile. (Onlinefi gure in color.)

30. First two abdominal tergites yellowish brown, remainder dark brown to black, contrasting; beard, thoracic hairs, and anterior marginal abdominal hairs bright creamy yellow to golden, contrasting with dark brown to black scutum. Northeastern Queensland. . . . . *aureohirta* (Ricardo 1900)

    Abdomen reddish brown to black; beard and pleural hairs paler creamy yellow; anterior marginal abdominal hairs cream to white (Figs. 9 and 10). Southeast Queensland, New South Wales, and Australian Capital Territory . . . 31

31. Scutum reddish to deep brown; abdomen, rather dark concolorous reddish brown to black, without median pale hairs or black vitta . . . . . *quadrimacula* (Walker, 1848)

    Scutum dark brown to greyish black; abdomen with pale brown anterior tergites contrasting to darker black posterior, and with creamy or yellowish median hairs 32

32. Scutum blackish brown, with conspicuous postalar tuft noticeably contrasting to ground color; abdomen shining, reddish brown, with a median, narrow, sometimes incomplete, black vitta . . . . . *subcontigua* (Ferguson 1921)

    Scutum blackish gray, postalar tuft less obvious (Figs. 9 and 10); abdomen duller and less shining, with a median creamy yellow or white vitta at apices of tergites 33

33. Beard and pleural hairs creamy yellow; scutum shining blackish gray; wings brownish, with obvious brown bifusciate wing patterns, and yellow radial area of basal cells (plate onefi g. 7); abdomen black, with black posterior noticeably contrasting to lighter brown anterior tergites, with dull cream apical median hairs . . . . . *lasiophthalma* (Macquart, 1834)

    Beard and pleural hairs creamy white (Figs. 9 and 10); scutum dull gray; wings greyish, without obvious bifusciate wing pattern and yellow radial area of basal cells; abdomen yellowish brown with darker posterior tergites not greatly contrasting those anteriorly, with creamy yellow apical median hairs . . . . . *wiegmanni* Lessard, sp. nov.

New species descriptions

Scaptia (*Pseudoscione*) *occidentalis* Mackerras, 1960, new status.

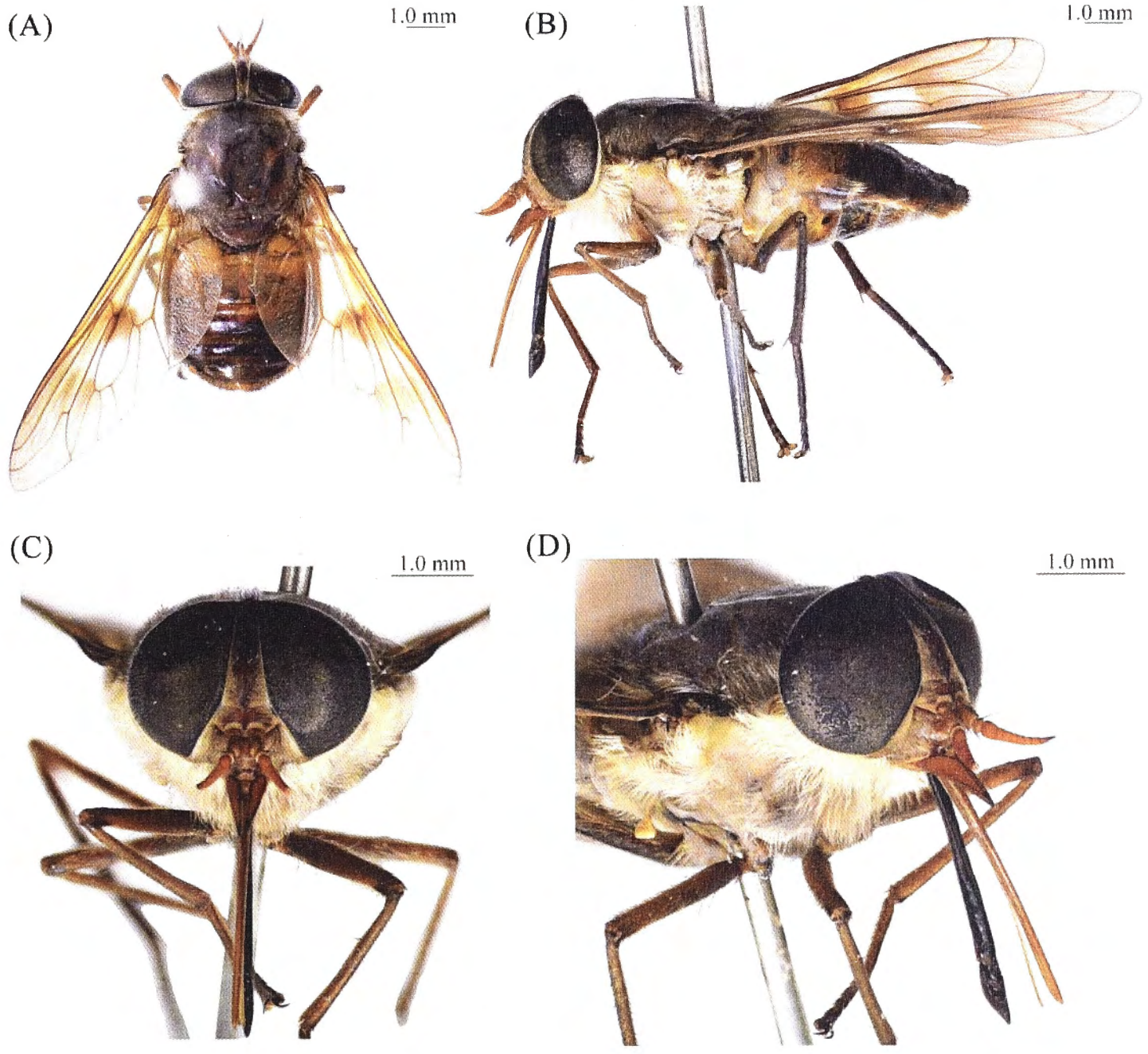

Fig. 7. *Scaptia* (*Pseudoscione*) *turcatelae* Lessard, sp. nov. Holotype female. (A) Dorsum. (B) Side. (C) Front. (D) Profile. (Onlinefi gure in color.)

Scaptia (*Pseudoscione*) *guttipennis occidentalis* Mackerras, 1960. Originally described as a subspecies of *Scaptia* (*Pseudoscione*) *guttipennis guttipennis* (Ferguson 1924), hereby raised to species.

Type Material. Holotype female, WA, Dryandra, 14-X-1954, J.H. Calaby (ANIC). Allotype male, WA, 6 miles N of Watheroo, 11-IX-1952, McIntosh and Calaby (ANIC).

Remarks. Distinguished from *Scaptia* (*Pseudoscione*) *guttipennis* by the differences mentioned in Mackerras (1960, pp. 97–100), specifically in modifications to the genitalia and body coloration, having a yellow beard and upper pleural hairs, as well as the distal four flagellomeres being blackish brown sharply contrasting the basal flagellomeres. The morphological variation between the former subspecies is equivalent to species-level differences in the context of the genus, and is hereby raised to species.

Scaptia (*Pseudoscione*) *baylessi* Lessard, sp. nov.
(Fig. 3)

Type Material. Holotype female, Qld, Bunya Mountains National Park, 11–13-XII-1979, G. Daniels and M.A. Schneider (UQIC #97075). Paratype females (2) same data as for holotype (UQIC #97074 and 97076).

Diagnosis. A medium sized (mean length 11.5 mm) dark member of the concolor subgroup, superficially similar to *S.* (*Ps.*) *aureohirta* with shorter palpi less than one third the length of proboscis shaft, with bifusciate wing patterns as in *S.* (*Ps.*) *quadrimacula*, but diagnosed by its smaller size, reduced narrow wing bands, concolorous dark greyish black scutum and abdomen, with hairs sparse yellow on scutum and creamy white on apical margins offi rst and second abdominal tergites. Differentiated from *S.* (*Ps.*) *lasiopthalma* by its blackish brown femora and overall darker coloration.

Female. Mean length 11.5 mm (SD 0.6 mm, range 11–12 mm).

Head. Eyes with brown hairs above, cream below and at sides. Frons diverging index 3.3, greyish brown at margins, slightly raised and darker brown at center, with dark brown hairs; ocellar tubercle slightly raised, dark brown to greyish, with dark brown to black hairs. Subcallus greyish brown, paler laterally, occasionally worn to dark brown at center, hairs sparse; parafacials greyish brown, darkening below, hairs creamy yellow

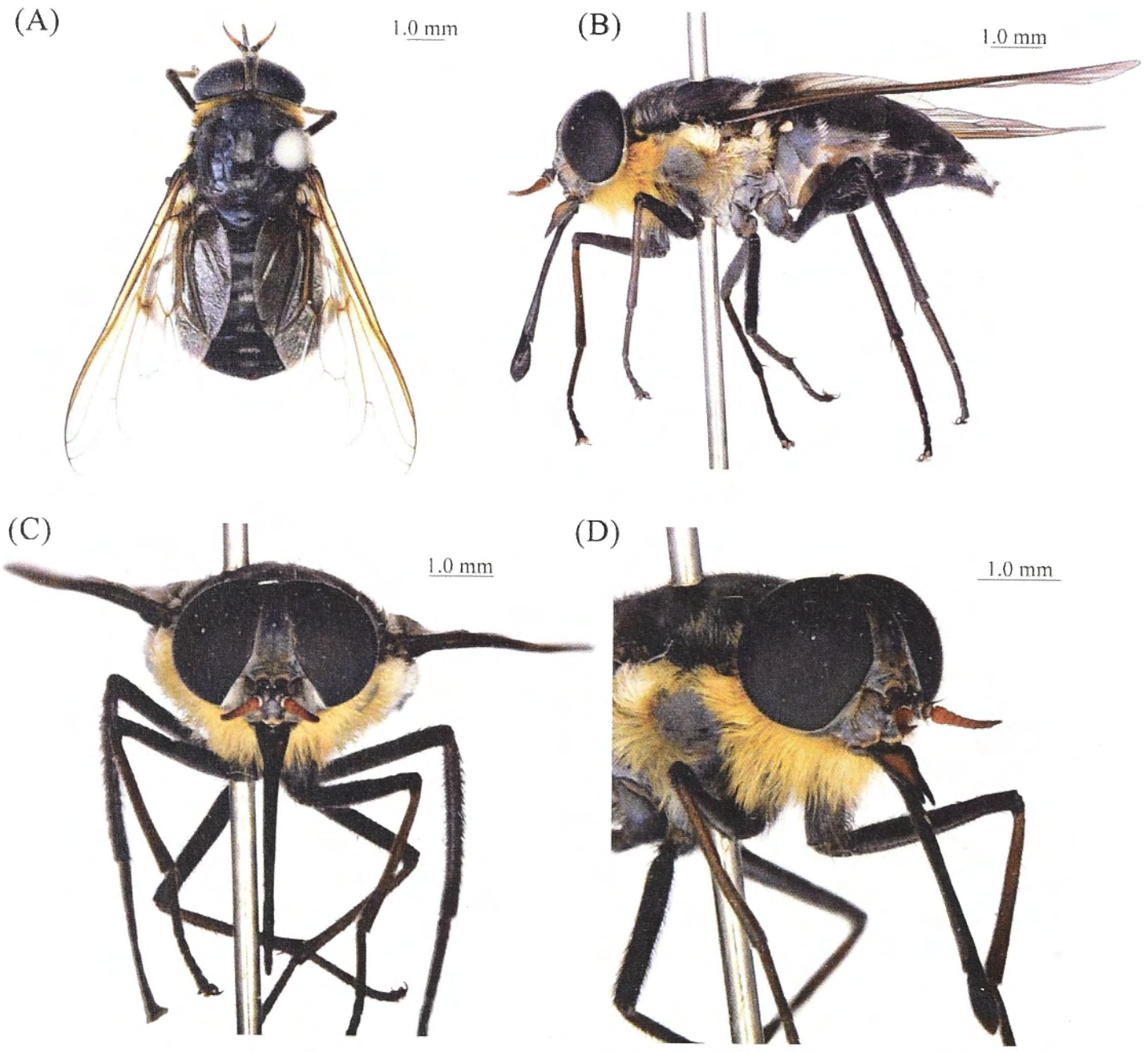

Fig. 8. *Scaptia (Pseudoscione) turneri* Lessard, sp. nov. Holotype female. (A) Dorsum. (B) Side. (C) Front. (D) Profile. (Onlinefi gure in color.)

dorsally, darker brown toward lower half and creamy yellow toward lower margins; face rather shiny, greyish brown laterally and dark brown below antennae, hairs creamy yellow at sides and dark brown below each antennae.

Antennae. First and second segments light brown, hairs mostly dark brown with some cream below; third bright yellow to orange, sometimes darkening at extreme tip.

Palpi. Slightly less than one third length of proboscis shaft;fi rst segment dark brown, hairs creamy yellow; second dark brown at margins with short black hairs, with a bright orange to brown concave bare area. Beard cream to pale yellow.

Thorax. Scutum and scutellum dark gray to black with a slight bluish hue and without indications of vittae, disc hair sparse yellow; notopleural hairs mixed black and golden yellow; supra- and postalar tufts dense, mixed with yellow and black, hairs mainly yellow on scutellum. Pleura light gray, occasionally brown where worn, with hairs predominantly cream to yellow.

Legs. Coxae gray, hairs dull cream to yellow above and black below; femora dark brown to black, tibiae and tarsomeres brown, slightly darker on hind pair; hairs predominantly black, with additional pale yellow hairs on femora, and a yellow to reddish brown zone on fore and hind tibiae and tarsomeres.

Wings. Brownish gray, more yellowish anteriorly and slightly darker toward the basal cells, deep brown for almost the entire radial area from the fork of R_5 to the tip of R_{2+3}, with the dark color diffusing into the brownish gray apical area, bands at both sides of discal cell appearing narrow and reduced. Veins yellowish brown; R_4 angulate without appendix; cell R_5 narrowly open.

Abdomen. Uniformly dark gray to black, with a slight bluish hue, hairs short black on disc, with a variable median zone of creamy white hairs at apices of all tergites that is more pronounced on posterior tergites; lateral hairs dull cream on tergites 1 and 2, black on 3 and 4, tergite 5 black at base and dull cream apically, with remainder of tergites forming a sparse dull cream tuft.

Venter. First sternite greyish brown becoming more creamy brown toward margins, hairs cream, remainder of sternites dark brown to black with predominantly short dull cream hairs.

Remarks. Mackerras (1960) had identified two specimens of the species from Boompa, Queensland, held in the ANIC, which were in poor condition and

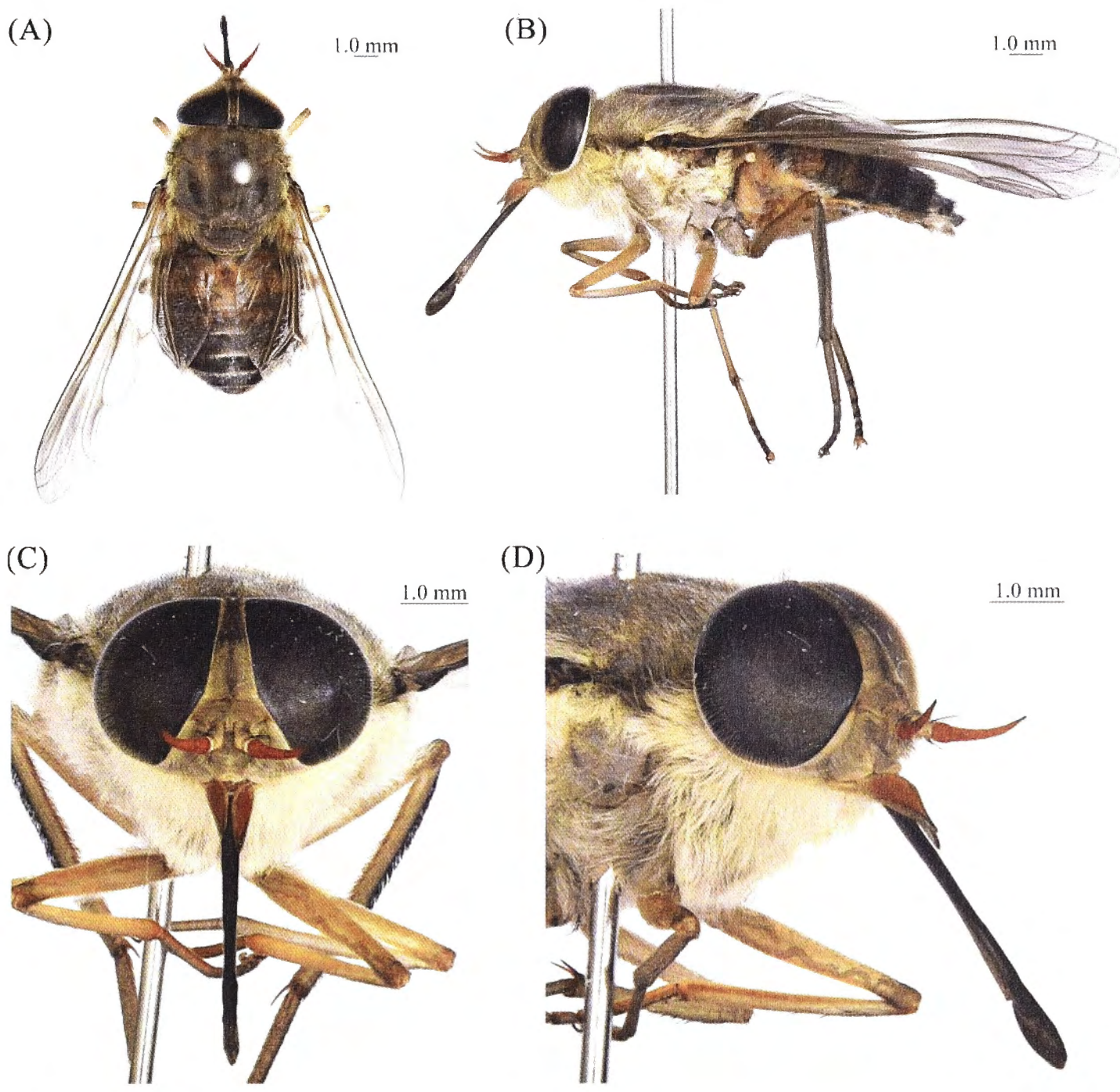

Fig. 9. *Scaptia* (*Pseudoscione*) *wiegmanni* Lessard, sp. nov. Holotype female. (A) Dorsum. (B) Side. (C) Front. (D) Profile. (Onlinefi gure in color.)

originally thought to be dark variants of *S.* (*Pseudoscione*) *lasiophthalma.*

Distribution. South-eastern Queensland (Fig. 2).

Etymology. The specific epithet is in honor of Keith Bayless for his contribution to Tabanidae systematics.

Scaptia (*Pseudoscione*) *casseli* Lessard, sp. nov. (Fig. 4)

Type Material. Holotype female, Qld, Mount Misery, SW Cooktown, 15° 52′ S 145° 13′ E, 867 m, 20-I-1994, G. Daniels, A. Daniels, and R. Eastwood (GDCB #21857). Paratype females (5) same data as for Holotype (GDCB #10951, 21854, 21855, 21856, and 21858).

Other Material Examined. Qld: female (1), Cape Tribulation, 3-I-1982, G. and A. Daniels (GDCB Reg #10950); female (1), Shiptons Flat, 31 km S Cooktown, rainforest, 15° 47′ S 145° 13′ E, 21-I-1994, G. Daniels, A. Daniels, and R. Eastwood (GDCB Reg #10952).

Diagnosis. A rather small species (mean length 11 mm) similar to *S.* (*Ps*) *baylessi*, with bifusciate wing patterns, uniformly dark brown abdomen, and palpi less than one third of the proboscis shaft, but separated by its light brown scutum with traces of vittae, creamy white beard and pleural hairs, and brown femora.

Female. Mean length 11 mm (SD 0.7 mm, range 10–12 mm).

Head. Eyes with short pale brown hairs. Frons diverging, index 3.4, greyish brown toward margins, slightly raised at center and dark brown where worn, hairs brown; ocellar tubercle slightly raised, greyish brown with long dark brown hairs. Subcallus fawn brown, lighter at base of antennae and eye margins; parafacials greyish fawn, becoming darker brown toward lower margins, hair light brown, occasionally with cream hairs near the mid regions and creamy white toward the lower margins; face fawn brown, darker brown near center, hairs dark brown near lateral margins.

Antennae. First and second segments light brown, hairs dark brown; third bright orange to yellow, vaguely darkening at extreme tip.

Palpi. Shorter than one third length of proboscis shaft;fi rst segment light brown, hairs dark brown api-

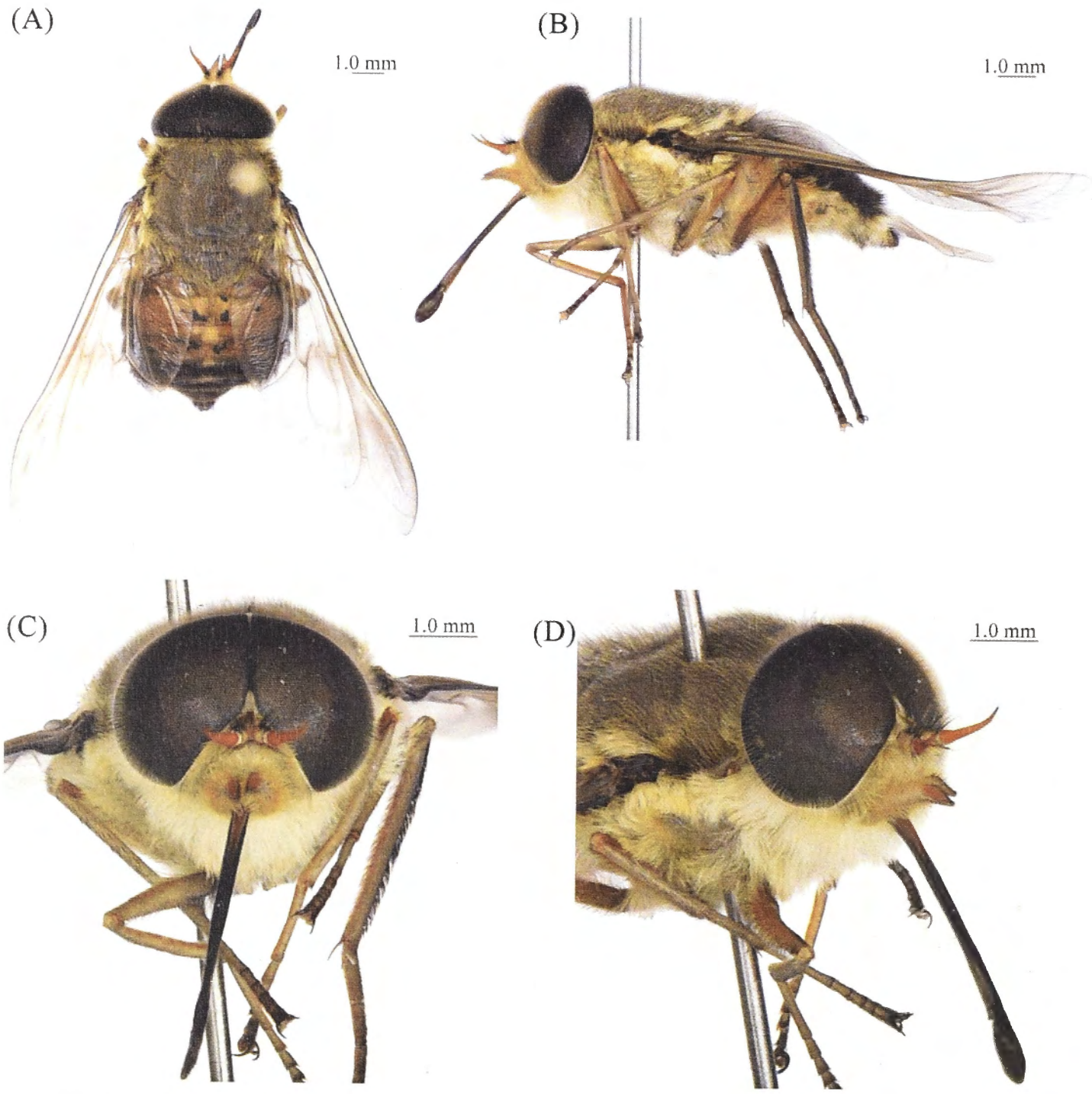

Fig. 10. *Scaptia* (*Pseudoscione*) *wiegmanni* Lessard, sp. nov. Paratype male. (A) Dorsum. (B) Side. (C) Front. (D) Profile. (Onlinefi gure in color.)

cally and creamy white near base; second orange brown with concave bare area, marginal hairs dense, short black. Beard creamy white.

Thorax. Scutum greyish brown with extremely faint dorsocentral lines that do not exceed the transverse suture, lateral margins only slightly lighter brown; disc hairs mixed with dull yellow and brown, brown at pronotum; notopleural tuft long black with some appressed golden brown hairs; supra- and postalar tufts mixed with creamy white and black; scutellum dark greyish brown at medial base with bluish hues, lighter brown at apical margins, hairs predominantly black with occasional pale yellow hairs. Pleura light gray to yellowish brown, hairs creamy white.

Legs. Coxae light gray to yellowish brown, mixed with creamy white and dark brown to black hairs that are densest on fore coxae; femora yellowish brown with predominantly black hairs, dorsal hairs white on basal two thirds of hind and mid femora; tibiae and tarsomeres yellowish brown, darker brown on hind pair, hairs predominantly short black, with golden brown ventral zone on fore legs.

Wings. Brownish gray, more yellowish anteriorly and with clearer areas at the basal and discal cells that further separate the two darker markings either side of the discal cell; deep brown for almost entire radial area from fork of R_5 to tip of R_{2+3}, the darker color diffuses into the brownish gray color apically; veins yellowish brown; R_4 angulate; cell R_5 narrowly open or closed with extremely short petiolate.

Abdomen. Uniformly dark brown with greyish blue hue, lighter brown onfi rst and second tergites; disc hairs dense black, with evanescent creamy white medial zone and apical bands on tergites 3 onwards; lateral hairs creamy white on most tergites except for three and four which are mixed with additional black hairs.

Venter. Sternite one light greyish brown with cream hairs, sternite two yellowish brown with some dark brown to black incursions, remainder of sternites becoming darker brown apically; disc hairs dark brown, with apical bands of cream hairs on all sternites.

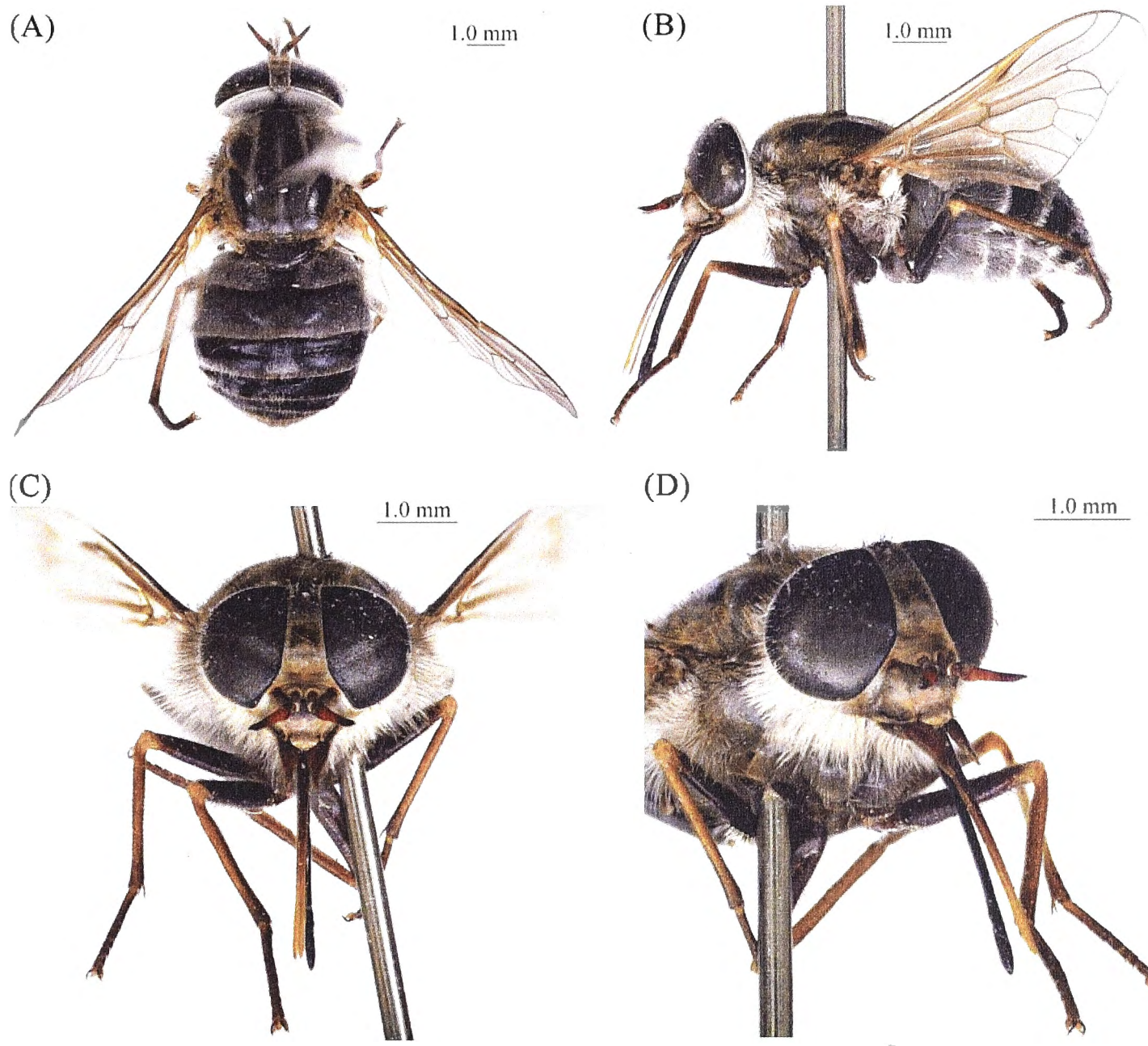

Fig. 11. *Scaptia* (*Pseudoscione*) *mackerrasi* Lessard, sp. nov. Holotype female. (A) Dorsum. (B) Side. (C) Front. (D) Profile. (Onlinefi gure in color.)

Distribution. North-eastern Queensland, between Cape Tribulation and Cooktown (Fig. 2).

Etymology. This specific epithet is in honor of Brian Cassel for his kind technical assistance in Diptera systematics.

Scaptia (*Pseudoscione*) *moritae* Lessard, sp. nov.
(Figs. 5 and 6)

Type Material. Holotype female, NSW, Boonoo Boonoo Falls, via Boonoo Boonoo, 24-I-1966, B. Cantrell (UQIC #97070). Paratype female (1) same data as Holotype female but collected by T. Wier (UQIC #97071). Paratype male (1) same data as for Holotype (UQIC #97072).

Other Material Examined. Female (1), Qld, Tinnanbar, 2.5 km S, 25° 47′ S 152° 53′ E, 10 m, 9-X-2002, Burwell, Cook and Wright, MV Light (QM).

Diagnosis. A medium sized (mean length 11.3 mm, SD 1.3 mm, range 11–13 mm), light brown species with creamy white beard, most similar to *S.* (*Pseudoscione*) *concolor,* but distinguished by broader and more dorsally ridged palpi, less obvious bifusciate wing patterns, lighter greyish brown thorax without red tinting, contrasting with darker brown abdomen with distinct pale medial stripe at center of all tergites.

Female. Mean length 12 mm (SD 1.4 mm, range 11–13 mm).

Head. Eyes with dense brown hairs. Frons diverging, index 2.7, slightly raised at center, brownish fawn, paler at margins, with brown hairs, ocellar tubercle dark brown, slightly raised with long dark brown hairs. Subcallus brownish fawn, paler laterally and without hairs; parafacials brownish fawn, with long dark brown hairs; face slightly gray to brownish fawn, slightly shining with long dark brown hairs.

Antennae. Scape and pedicel brownish fawn with long black hairs; flagellomeres uniformly bright yellowish brown, darkening at extreme tip of apical flagellomere.

Palpi. First segment brownish fawn with dark brown to black hairs above and cream below; second segment over one third length of proboscis shaft, slightly ridged dorsally, with bare area yellowish to orange brown, almost flat with short black marginal hairs. Beard creamy white.

Thorax. Scutum and scutellum uniformly light gray to brownish fawn, paler anteriorly, with erect hairs on disc brown, suppressed hairs paler yellowish brown and hairs on posterior edge of scutum and scutellum long pale yellow to light brown; notopleural hairs predominantly dull golden brown, with some black

ones; supra-alar tuft long, creamy golden brown, mixed with sparse black hairs, postalar tuft predominantly creamy white with some pale yellowish brown hairs anteriorly, sometimes with sparse black hairs. Pleura greyish white to pale yellowish brown, with creamy white hairs.

Legs. Coxae greyish white to pale yellowish brown, with hairs creamy white above and long black below. Femora, tibiae, and tarsomeres light yellowish brown, becoming darker brown at apices; femora hairs mostly blonde with some black ventrally, fore and mid tibiae hairs short blonde to yellowish brown with intermittent black dorsal hairs, hind tibiae with pale yellowish brown hairs, all tarsomeres with short pale yellowish brown hairs.

Wings. Greyish, clearest at basal and discal cells, more yellowish radially, bifusciate wing pattern less obvious with second radial band at tip of R_{4+5} diffusing into the darker gray apical color; veins yellowish brown; R_4 angulate, without appendix; cell R_5 narrowly open or closed with extremely short petiole.

Abdomen. Brown, somewhat shining, with characteristic light yellowish brown medial stripe down center of all tergites, and some vague darker brown markings; hairs on disc predominantly yellow to golden brown with occasional brown hairs densest at lateral margins offi rst two tergites; marginal hairs cream to yellowish brown onfi rst two tergites, yellowish to golden brown on remaining tergites.

Venter. Shining yellowish brown with darker brown incursions and vague, rather sparse black markings, hairs mostly cream with some black in median zone.

Male. Slightly smaller (mean length 10.5 mm, SD 0.7 mm, range 11–12 mm) and hairier than female, eyes with upper facets not obviously enlarged. First segment of palpi pale yellowish brown with creamy yellow hairs; second segment subcylindrical, brownish fawn with dull orange brown bare area, hairs mostly short black with some lighter brown below at base.

Remarks. The Paratype female has darker pleura, frons, parafacials, and hairier face. This is interpreted as intraspecific variation because the specimen was collected at the same locality and time, and possesses the main features of the medial abdominal stripe and structural modification of the palpi.

Distribution. South-eastern Qld to north-eastern NSW (Fig. 2).

Etymology. The specific epithet is in honor of Shelah Morita for her systematic work on the horse fly subfamily Pangoniinae.

Scaptia (*Pseudoscione*) *turcatelae* Lessard, sp. nov. (Fig. 7)

Type Material. Holotype female, NE Qld, 3–5 km W of Cape Tribulation (Sites 6–10), 29-XII-1982 to 3-I-1983, 500–780 m, G.B. Monteith (QM).

Diagnosis. A small (length 11 mm) species with cream beard, superficially similar to *S.* (*Pseudoscione*) *casseli*, but distinguished by its dark greyish brown scutum, wings with the second band on the discal cells being less pronounced than the darker band on the basal cells, and with a more shining abdomen with golden brown anterior tergites contrasting to the darker brown posterior.

Female. Length 11 mm.

Head. Eyes with dense brown hairs on upper half, pale cream on lower half. Frons diverging, index 3.0, brown, paler fawn along eye margins and darker at worn areas near center, hairs short brown; ocellar tubercle greyish brown, raised, hairs long black. Subcallus fawn brown, yellowish brown at worn center, hairs inconspicuous; parafacials fawn brown, hairs cream dorsally and brown ventrally; face shining, orange brown, hairs pale cream.

Antennae. Scape and pedicel orange brown, hairs predominantly black with some pale brown on lateral and ventral sides of scape; flagellomeres orange brown, darkening at extreme tip.

Palpi. First segment fawnish brown, hairs cream; second segment over one third the length of the shaft of the proboscis, with almost flat orange brown bare area, marginal hairs short black. Beard creamy white.

Thorax. Scutum and scutellum greyish brown, darker brown where worn, with a bluish gray dusting on the anterior of prescutum, brown where worn, with pale brown dorsocentral lines and lateral areas, scutellum lighter brown along posterior margin; disc hairs black, some cream on posterior margins of scutum and scutellum; notopleural hairs long black; supra- and postalar tufts black anteriorly and creamy white posteriorly, conspicuous. Pleura pale gray to creamy brown, hairs predominantly creamy white, somewhat yellowish along dorsal margin of anepisternum.

Legs. Coxae pale creamy brown, hairs long, creamy white above and black below. Femora dark brown on basal quarter of fore leg and basal three quarters of mid and hind leg, lighter brown elsewhere, hairs creamy yellow, mixed with black on ventral side of mid and hind legs; tibiae and tarsomeres brown on fore and mid legs with hairs black, fore legs with a pale brown ventral zone, hind legs dark brown to black with dense black hairs.

Wings. Brownish gray, yellowish toward radial area of basal cells, clearer areas at basal cells and distal half of discal cells, with two bands at apices of basal and discal cells, with the latter being more evanescent and diffusing from the discal cell into the brownish gray apical color. Veins brown; R_4 angulate without appendix; cell R_5 closed with short petiole.

Abdomen. Shining, golden brown onfi rst two tergites, contrasting to the darker brown to black posterior tergites with obscure incursions of pale golden brown, hairs on disc black, without obvious vittae, some sparse medial tufts on apices of tergites 2–4, marginal hairs on first tergite predominantly pale creamy yellow with some black, tergites 2 and 3 with predominantly pale creamy yellow hairs with some black on third, entirely black on fourth, mixed pale creamy yellow and black onfi fth, with obvious pale creamy yellow tuft on sixth.

Venter. Shining, golden brown, with a narrow, medial dark brown distal area on second sternite broadening outwards on remaining sternites, with obscure

golden brown incursions on posterior sternites, hairs on disc predominantly pale golden brown.

Distribution North-eastern Queensland (Fig. 2).

Etymology. This specific epithet is in honor of Maureen Turcatel for her work on the tabanid subfamily Chrysopsinae.

Scaptia (*Pseudoscione*) *turneri* Lessard, sp. nov. (Fig. 8)

Type Material. Holotype female, N.E. Qld, Mt Finnigan summit slabs, 1,100 m, 15° 49′ S 145° 17′ E, 20–21-XI-1998, C.J. Burwell (QM). Paratype females (5) same data as for Holotype; Paratype female (1) same location and altitude as Holotype, but with collected on 20–22-XI-1998 by G. Moneith, P. Bouchard, and A. O'Toole (QM); Paratype females (6), Qld, Mt Finnigan summit, S Cooktown, rainforest, 1,140 m, 28–30-XI-1985, G. Monteith, D. Cook, and L. Roberts (UQIC #97321, 97322, 97323, 97324, 97326, and 97341).

Other Material Examined. N.E. Qld: female (1), 3–5 km W of Cape Tribulation, 500–780 m, 29-XII-1982 to 3-I-1983, G.B. Moneith (UQIC #97337); females (5), Cardwell Range, Upper Broadwater Creek Valley, 700–800 m, 17–21-XII-1986, Monteith, Thompson, and Hamlet (QM); female (1), C.R.E.B. track, 16.5 km N Daintree, rainforest, 520 m, 27-XII-1985, D.K. Yeates (UQIC #97084); female (1), Mt Pieter Botte, 950 m, 16° 04′ S 145° 24′ E, 21-XI-1993, Monteith, Janetzki, Roberts, and Cook (QM); female (1), North Bell Peak, Malbon Thompson Ra., 800–1,000 m, 19–22-XI-1990, Monteith and Thompson (QM); females (3), Upper Boulder Creek via Tully, 650–900 m, 24–27-X-1983, Monteith, Yeates, and Thompson (QM).

Diagnosis. A medium sized species (mean length 11.5 mm), most similar to *S.* (*Ps.*) *baylessi*, but distinguished by its dull brown antennae and palpi, dense pale creamy yellow hairs on parafacials and creamy white hairs on posterior half of pleura. This species is the only member of *concolor* group without obviously banded patterns of the wing, possessing only a single evanescent brown marking at the apices of basal cells.

Female. Mean length 11.5 mm (SD 0.7 mm, range 10–12 mm).

Head. Eyes with pale brown hairs above and creamy yellow ones below. Frons almost parallel above the dorsal third and strongly diverging at base, index 3.0, slightly raised at center, greyish along margins, slightly raised and black at center, hairs black; ocellar tubercle slightly raised, black with black hairs. Subcallus gray along margins, brownish gray at center and base of antennae, worn areas at center black, hairs sparse, pale creamy yellow; parafacials greyish brown, hairs dense pale creamy yellow, occasionally mixed with black on lower third, yellow at extreme lower margin; face somewhat shining, gray at margins and dark brown at center, short yellowish brown hairs obscured by dense hairs of antennae and parafacials.

Antennae. First and second segment dark brown to black with gray tomentum, second segment slightly lighter, both with long black hairs dorsally and long laterally, with pale yellow hairs ventrally; flagellum dull orange brown, darkening at tip.

Palpi. First segment dark brown with gray tomentum, hairs predominantly yellow; second segment one third the length of the proboscis shaft, dark brown to black with dull orange brown bare lateral concavity, marginal hairs short black. Beard yellow.

Thorax. Scutum and scutellum shining, dark greyish black with a bluish hue, scutum with indications of gray dorsocentral lines and paler anterior and lateral margins; disc hairs black; notopleural hairs black; supra-alar tuft black, postalar tuft dense, conspicuous, predominantly cream posteriorly with some sparser black anteriorly. Pleura gray, hairs predominantly yellow, hairs of anepisternum yellow at center and cream at margins, katepisternum tuft yellow above and cream below, katatergite tuft cream.

Legs. Coxae gray, hairs black at lower margins, yellow dorsally on fore leg, and cream on mid and hind legs; femora dark brown to black, hairs mostly black, with cream dorsally on hind leg and basal third of mid leg; tibiae and tarsomeres brown, hind legs darker, hairs predominantly black, with lighter brown ventral zone on all tarsomeres and front tibiae, darker on mid legs.

Wings. Hyaline to greyish, with yellowish radial area along costal cell near base, and with a single brown marking at apices of basal cells; veins yellowish brown; R_4 angulate, sometimes with trace of appendix; cell R_5 open.

Abdomen. Shining, uniformly dull black with a slight bluish hue, somewhat lighter onfi rst two tergites; hairs on disc black, with obvious white medial tufts on apices of tergites 2 onwards, conspicuous pale creamy white lateral tufts on tergites 1, 2, 5, and 6, lateral tufts completely black on tergites 3, 4, and 7.

Venter. Sternite one greyish black with creamy white hairs, remainder dark brown to black, with lighter brown lateral margins on basal sternites; hairs on disc black, with creamy white hairs forming bands at apical margins of all sternites.

Distribution. North-eastern Queensland, between Cape Tribulation and Cooktown (Fig. 2).

Etymology. This specific epithet is in honor of Steven Turner for his contribution to Diptera systematics.

Scaptia (*Pseudoscione*) *wiegmanni* Lessard, sp. nov. (Figs. 9 and 10)

Type Material. Holotype female, NSW, Bawley Point, 35° 30′ S 150° 24′ E (GPS), 22-XI-1999, DCF Rentz (ANIC). Paratype females (7), same data as for Holotype, with the following differences: female (1), 3-XII-1997, DCF Rentz; female (1), 6-II-1998, DCF Rentz and K McCarron; female (1), 18-XII-1999, DCF Rentz; females (2), 21-I-2000, DCF Rentz; female (1), 4-I-2001, DCF Rentz; female (1), 25-I-2001, DCF Rentz. Paratype males (6), same location as Holotype but with the following differences: males (2), 6-I-1998, DCF Rentz and K McCarron; male (1), 22-I-1994, DCF Rentz and K McCarron; male (1), 2-XII-1994, DCF Rentz and K McCarron; male

(1), 1-I-2001, DCF Rentz; 1 male, 26-I-2001, DCF Rentz.

Other Material Examined. Female (1), NSW, Depot Beach, 10 miles NE of Batemans Bay, 30-XII-1967, IFB Common (ANIC); females (2), NSW, Mimosa Rocks NP, Gillards Campsite, 1-I-1996, MV Lamp and J Bugeja (ANIC).

Diagnosis. A robust species (mean length 13.8 mm, SD 0.9 mm, range 13–16 mm), superficially similar to *S. (Ps.) lasiopthalma* with relatively long palpi at least one third the length of the proboscis shaft, but separated by its creamy white beard and pleural hairs, pale greyish brown scutum, dull yellowish brown abdomen with basal tergites not sharply contrasting distal segments, bifusciate wing pattern less conspicuous and without obvious yellow basal cells.

Female. Mean length 13.9 mm (SD 1.0 mm, range 12–16 mm). Eyes with dense brown hairs above, more creamy yellow below. Frons diverging, narrow, frons index 4.0, slightly raised at center, greyish brown, fawn at margins, hairs short brown, ocellar tubercle slightly raised, brown with long black hairs. Subcallus pale fawn brown with pale creamy hairs at lateral margins; parafacials creamy fawn with relatively dense, long, dull creamy yellow hairs above and some black below; face pale brown to fawn, somewhat shining with long black hairs at center and pale yellow to cream at margins.

Antennae. Scape and pedicel brownish fawn, hairs predominantly black with some dull cream yellow ventrally on both segments; flagellomeres bright orange brown, darkening at extreme tip.

Palpi. First segment fawnish brown with cream hairs; second fawnish brown at margins with bright orange brown lateral concave bare area, marginal hairs short black. Beard pale yellow to cream.

Thorax. Scutum and scutellum greyish brown, with indications of gray medial and dorsocentral lines and lateral margins, hairs on disc mixed with erect black and appressed dull creamy yellow ones, densest in front of scutellum; notopleural tuft conspicuous, mixed pale creamy yellow and black; supra-alar and postalar tuft pale creamy yellow with some black hairs above. Pleura pale greyish cream to fawnish brown, hairs entirely pale yellow to cream.

Legs. Coxae pale greyish cream to fawnish brown, hairs pale yellow to cream, mid and hind coxae with some black hairs below. Fore and mid femora, tibiae and tarsomeres bright yellowish brown, slightly contrasting with darker brown hind legs, hairs predominantly pale yellowish cream with some black ventrally at base, hairs on tibiae and tarsomeres golden brown ventrally and black dorsally, hairs densest on hind legs.

Wings. Gray, clearest at basal and discal cells, base and costal cells without obvious wing yellow staining, the two greyish brown bands extending across the apices of the basal and discal cells appear evanescent and sometimes discreet, with the banding at the discal cell diffusing into the gray apical color. Veins pale yellowish brown; R_4 angulate, without appendix; cell R_5 closed at margins, with or without short petiole.

Abdomen. Dull yellowish brown, not obviously shining, with irregular black markings becoming more frequent from second tergite onwards, posterior tergites darker brown, not entirely black or strongly contrasting to basal tergites; hairs on disc black, with pale yellowish cream medial vittae on apices offi rst tergites, expanding into an apical fringe on remaining tergites, marginal hairs dense, predominantly cream onfirst and second tergites, mixed with black above and cream below on tergites 3–5, pale yellowish cream on 6, mixed pale yellowish cream and black on tergite 7.

Venter. First sternite creamy brown, remaining sternites bright yellowish brown with somewhat irregular black markings along the lateral margins and median zone, occasionally darkening apical sternites; hairs on disc cream with a black medial zone on sternites two onwards.

Male. Similar to female but slightly smaller in size (mean length 13.5 mm, SD 0.5 mm, range 13–15 mm), hairier and with hairs that are only slightly more yellowish, dull, but not as distinctly bright yellow as in the males of *S. (Ps.) lasiophthalma.* Eyes with upper facets not obviously enlarged. Palpi subcylindrical, pale yellowish cream with bright orange brown bare area with black marginal hairs. Wings greyish, without yellow coloration on basal cells and with only slightly more obvious banding than the female. Abdomen dull yellowish brown, with less defined apical fringes of pale creamy yellow hairs, apical tergites are not uniformly black, but are instead a mottled yellowish brown.

Distribution. South-eastern NSW (Fig. 2).

Etymology. This specific epithet is honor of Brian Wiegmann for his contribution to Diptera systematics.

Scaptia (Pseudoscione) mackerrasi Lessard, sp. nov. (Fig. 11)

Type Material. Holotype female, NT, 39 km E of Alice Springs, 25-IX-1978, M.S. Upton and R.A. Barrett (ANIC). Paratype females (2), same data as for Holotype (ANIC); females (3), NT, 39 km E of Alice Springs, 23.41 S 134.15 E, 25-IX-1978, J.C. Cardale (ANIC); female (1), same data as previous with the exception of 26-IX-1978 (ANIC); females (2), NT, 39 km E of Alice Springs, 5-X-1978, D.H. Colless (ANIC); females (4), same data as previous, with the exception of 6-X-1978 (ANIC).

Other Material Examined. NT: female (1), 33 km WNW of Alice Springs, 23.36 S 133.34 E, 30-IX-1978, J.C. Cardale (ANIC); female (1), 33 km WNW of Alice Springs, 30-IX-1978, M.S. Upton and R.A. Barrett (ANIC); female (1), 53 km E by N of Alice Springs, 6-X-1978, D.H. Colless (ANIC); female (1), same data as previous, malaise trap (ANIC); female (1), 30 km NW by W of Alice Springs, 7-X-1978, D.H. Colless (ANIC); females (2), Amadeus Basin, 29-IX-1962, P. Ranford (ANIC); female (1), Finke Gorge Nat. Pk. Amphitheatre, 5-IX-1973, G. Griffin (ANIC); female (1), James Ranges, 24.15 S 133.26 E, 22-IX-1978, M.S. Upton and R.A. Barrett (ANIC); female (1), same data as previous, with the exception of J.C. Cardale (ANIC); female (1), Kings Canyon, 29-VIII-1973, K.L.

Taylor (ANIC); females (3), Mt Brunonia, Deep Well Station, S of Alice Springs, 26-VII-85, K. Marsters (ANIC); females (2), same data as previous, with the exception of 27-VII-85 (ANIC); females (4), Mt Solitaire, 30 km NW by W of Alice Springs, 23.32S 133.38E, 29-IX-1978, J.C. Cardale (ANIC); female (1), Roe Creek, 12 km SW by W of Alice Springs, 23.46 S 133.46 E, 27-IX-1978, J.C. Cardale (ANIC); female (1), Todd River, 9 km N by E of Alice Springs, 23.38 S 133.53 E, 28-IX-1978, J.C. Cardale (ANIC); female (1), Waterhouse Range, 12-X-1978, D.H. Colless (ANIC). SA: females (2), Arcoona Ck., Gammon Ranges, at light, 17-IX-1956, G.F. Gross (SAM); female (1), Crest, Gammon Range, nr. Gammon Hills, 15-IX-1956, G.F. Gross (SAM); female (1), Flinders Ranges, Moolooloo, X-1915, J.W. Mellon (SAM); female (1), Italowie Gorge, hills above, 30-X-1955, E.T. Giles (ANIC).

Diagnosis. A small (mean length 9.5 mm), black species with cream beard, dark brown to black legs with pale brown knees, shining, concolorous dark brownish black scutum and abdomen, the latter having narrow golden brown bands on extreme apices of all tergites. Distinguished to all members of *S.* (*Pseudoscione*) by its more protuberant and bulging face, relatively short, pointed palpi with deep lateral concavity and strong scutal vittae.

Female. Mean length 9.5 mm (SD 0.7 mm, range 9–11 mm).

Head. Eyes with hairs dark brown above and paler brown below. Frons strongly diverging, index 1.9, greyish brown, worn areas at center darker brown, ventral margins golden fawn, hairs brown; ocellar tubercle dark brown, slightly raised, hairs long black. Subcallus fawnish brown, greyish along margins, hairs sparse creamy brown; parafacials greyish brown with creamy white hairs above and some darker brown below; face bulging to protuberant, shining, area below antennae dark brown with brown hairs, lateral margins more greyish with creamy white hairs.

Antennae. Scape and pedicel brown with gray tomentum, hairs dark brown; flagellum yellowish brown, darkening on apical four flagellomeres.

Palpi. First segment dark brown with dark brown hairs above and white below; second segment pointed and relatively short, less than one third the length of the proboscis shaft, brown with deep concavity and with sparse dark brown marginal hairs. Beard white.

Thorax. Scutum and scutellum shining concolorous black, with well pronounced gray median, dorsocentral vittae and lateral margins, more brown laterally behind transverse suture, hairs on disc brown, white hairs on anterior margin of prescutum, scutellum hairs long black; notopleural hairs sparse, black with some cream; supra- and postalar tufts sparse, mixed with brownish black and creamy white. Pleura dark greyish brown, with entirely creamy white hairs.

Legs. Coxae dark brown and slightly greyish, hairs predominantly dark brown on fore and mid pair and creamy white on hind legs. Femora dark brown to black, hairs long black with smaller golden brown zone on dorsal third of fore and mid legs, entirely creamy white on hind pair; tibiae and tarsi brown with predominantly brown hairs, with a pale golden brown ventral zone most obvious on fore legs.

Wings. Brownish gray, basal cells with rather vague darker brown markings at apices and with yellowish radial area, stigma obvious brown; veins yellowish brown; R_4 angulate, with or without appendix; cell R_5 closed, long petiolate.

Abdomen. Shining dark brown to black with narrow golden brown bands at extreme apices of all tergites, thefi rst three tergites with gray dusting, hairs on disc sparse and black,fi rst tergite with a medial black tuft and creamy white tufts adjacent the scutellum, remainder of tergites with evanescent median patches of creamy white hairs, marginal hairs entirely creamy white.

Venter. Dark greyish brown on all sternites with narrow golden brown bands on extreme apices, hairs predominantly creamy white.

Distribution. Southern NT around the Alice Springs region (Fig. 2). One specimen has been found from central eastern SA. This is over 1,200 km NW from the closest other member of *S.* (*Pseudoscione*), being the furthest inland species recorded for the genus and significantly extending the known distribution of *Scaptia* into central Australia.

Remarks. This curious species has been provisionally placed within *S.* (*Pseudoscione*) based on the proboscis length greater or equal to 1.5 times that of head height, distinctly diverging frons and relatively slender palpi with deep lateral concavity. However, it also shares defining characteristics of *S.* (*Plinthina*), including the strong scutal vittae, frons that is not raised at center, wings with obvious stigma, as well as a rotund and somewhat shorter flagellum that is more similar to *S.* (*Myioscaptia*). A case could be made to establish a new genus of Scionini comprising *S.* (*Pseudoscione*) *mackerrasi.* Moreover, *S.* (*Pseudoscione*) *mackerrasi* may be closest related to the ancient lineage of *Scaptia* that gave rise to *S.* (*Pseudoscione*), *S.* (*Myioscaptia*), and *S.* (*Plinthina*) known today. Moreover, the more protuberant and projecting face of the species also suggests a strong link to the South American genera *Fidena* and *Scione.*

Etymology. This specific epithet is in honor of Ian Mackerras for his dedication to the systematics of the Tabanidae.

Discussion

Morphological characters were successful in delimiting seven new species of Australian *S.* (*Pseudoscione*), in addition to raising one species that was previously described as a subspecies. The new species *S.* (*Pseudoscione*) *mackerrasi* Lessard, sp. nov. significantly extends the known distribution of *Scaptia* into central Australia. The nearest species of *Scaptia* is over 700 km NE of Alice Springs belonging to another subgenus, *Scaptia* (*Plinthina*) *arnhemensis* Lessard, 2011, collected from Musselbrooke Creek, Lawn Hill National Park, Queensland (Lessard and Yeates 2011; Fig. 1). Furthermore, *S.* (*Pseudoscione*) *mackerrasi*

Lessard, sp. nov. is >1,200 km NW from the nearest species within the same subgenus, *Scaptia* (*Pseudoscione*) *guttipennis* (Ferguson 1924), recorded from Cleve, South Australia. Given the large geographical isolation and differences in morphology, a case could be made to separate *S.* (*Pseudoscione*) *mackerrasi* Lessard, sp. nov. from its current provisional placement within *S.* (*Pseudoscione*) and establish a new genus of Scionini. This would be aided by future molecular analysis, which could also evaluate the generic limits of the morphologically distinct *S.* (*Pseudoscione*) divisions in Australia, New Zealand, and South America. Assuming that the subgenus were to be divided into its three geographically distinct genera, the name *Pseudoscione* Lutz, 1918 would apply to South American members, and *Copidapha* Enderlein, 1922 would become available for the Australian taxa.

Based on previous collection records from Australia, *Scaptia* was believed to be exclusively adapted to mild-temperate to subtropical environments (Mackerras 1960). Temperature and availability of soil moisture was further thought to restrict the current distribution of *Scaptia*, both regulating breeding behavior, larval development (although little is known regarding larval biology for the family), frequency of adult emergence, and sustainability of flowers for feeding (Mackerras 1960). However, the distribution records for *S.* (*Pseudoscione*) *mackerrasi* Lessard, sp. nov., coupled with the known members of *S.* (*Plinthina*) adapted to drier climates, demonstrate the ability of *Scaptia* to tolerate arid, drought prone environments subjected to extreme temperatures. It is expected that more species of *Scaptia* could await discovery from other remote and arid regions of Australia.

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Chapter Six

New species of the Australian horse fly subgenera *Scaptia* (*Scaptia*) Walker, 1850 and *Scaptia* (*Myioscaptia*) Mackerras, 1955 (Diptera: Tabanidae)

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New species of the hairy-eyed horse fly subgenera *Scaptia* (*Myioscaptia*) Mackerras, 1955 and *Scaptia* (*Scaptia*) Walker, 1850 (Diptera: Tabanidae) from Australia

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Abstract

New material has accumulated in several Australian Museums since Mackerras' extensive 1960's revision of the austral horse fly genus *Scaptia* Walker 1850, including one new species of *Scaptia* (*Scaptia*) Walker, 1850 and two new species of *Scaptia* (*Myioscaptia*) Mackerras, 1955. The new species are *Scaptia* (*Scaptia*) *aurinigra* Lessard, **sp. n.** and *Scaptia* (*Myioscaptia*) *collessi* Lessard, **sp. n.** both from Queensland, and *Scaptia* (*Myioscaptia*) *lambkinae* Lessard, **sp. n.** from Western Australia. All new species are described and illustrated. Additionally, an updated key to species of *Scaptia* (*Myioscaptia*) is provided and includes all eleven known species of the subgenus. One novel species significantly extends the known distribution of the genus over 700 km further NE into central Western Australia.

Key words: Pangoniinae, Scionini, morphology, descriptive taxonomy

Introduction

Australian horse flies (Diptera: Tabanidae) are important pollinators of *Eucalyptus, Leptospermum* and other myrtaceous plants (Johnson and Morita 2006; Tillyard 1926; Lessard and Yeates 2012b; Mackerras 1957, 1960; Morita 2008). The family is more disreputable for the biting behaviour of females that can lead to the mechanical transmission of microorganisms causing a myriad of diseases affecting livestock, native mammals and even humans (Foil *et al.*1984; Foil *et al.*1988; Foil 1989; Krinsky 1976; Reid *et al.*2001; Scoles *et al.*2008; Spratt 1972a, 1972b, 1974a, 1974b, 1975). The Australian species *Scaptia* (*Myioscaptia*) *calliphora* Mackerras 1955, *Scaptia* (*Myioscaptia*) *ferromontana* Daniels 2011, *Scaptia* (*Myioscaptia*) *inopinata* Fairchild & Mackerras 1977, *Scaptia* (*Myioscaptia*) *violacea* (Macquart 1850) and *Scaptia* (*Myioscaptia*) *bancrofti* (Austen, 1912) have all been reported to attack humans (Mackerras 1960), with the latter two also feeding on cattle (Mackerras 1960; Fairchild and Mackerras 1977; Daniels 2011).

The genus *Scaptia* usually comprises stout and hairy flies and is currently divided into seven subgenera, including *Lepmia* Fairchild 1969 (found in Brazil), *Pseudomelpia* Enderlein 1922 (Chile), *Myioscaptia* Mackerras 1955 (Australia), *Palimmecomyia* Taylor 1917 (Australia) and *Plinthina* Walker 1850 (Australia), along with the more widely dispersed and species-rich subgenera *Pseudoscione* Lutz in Lutz, Araujo & Fonseca 1918 (Australia, Argentina, Brazil, Chile, New Guinea and New Zealand) and *Scaptia* Walker 1850 (Australia, Chile, Peru, Bolivia, Argentina).

Australian members of *Scaptia* (*Scaptia*) are mostly solidly built species, with relatively short and strong legs, distinguished from other subgenera by the parallel frons, large pointed and sabre-like palpi, and short and thick proboscis with large well-developed labella. In contrast, the Australian subgenus *Scaptia* (*Myioscaptia*) comprises small and rotund species, usually semi-metallic or metallic in colour. Some species are obvious blowfly mimics, resembling the general appearance of the calliphorid genera *Calliphora* Robineau-Desvoidy, 1830 and *Lucilia* Robineau-Desvoidy, 1830, as well as the sound, and directionless, low level approach in flight (Nicholson 1927;

Mackerras 1955, 1960). Moreover, it is only one of three *Scaptia* subgenera to have known larvae and pupae described, with the larvae of some species having the unusual habit of developing in sandy cave floors, sandstone cliff ledges, as well as sometimes coexisting with ant lion larvae (English 1955; Mackerras 1955, 1960).

This study is part of a recent surge of taxonomic research currently being conducted on the Australian Tabanidae (Mackerras *et al.* 2008; Lessard and Yeates 2011, 2012a, 2012b). It has been over 50 years since Ian Mackerras' (1960) major revisions of the genus *Scaptia*. Since then, many new species have accumulated in collections around Australia, including two species that have been recently described. Three new species are named, illustrated and described herein, and an updated key to species for *S.* (*Myioscaptia*) is provided to include all eleven known species (Table 1). Don Colless collected the only specimen for one of the new species described below.

TABLE 1. Species list of the Australian horse fly subgenus *Scaptia* (*Myioscaptia*) Mackerras, 1955. Asterisk indicates type species.

Recognised species		
S. (*M.*) *calliphora* Mackerras, 1960	*S.* (*M.*) *inopinata* Fairchild & Mackerras, 1977	*S.* (*M.*) *nigroapicalis* Mackerras, 1960
S. (*M.*) *collessi* Lessard, **sp.n.**	*S.* (*M.*) *lambkinae* Lessard, **sp.n.**	*S.* (*M.*) *nigrocincta* Mackerras, 1960
S. (*M.*) *bancrofti* (Austen, 1912)	*S.* (*M.*) *muscula* (English, 1955)	*S.* (*M.*) *violacea* (Macquart, 1850)*
S. (*M.*) *gibbula* (Walker, 1848)		
S. (*M.*) *ferromontana* Daniels, 2011		

Materials and methods

Morphological terminology follows Mackerras *et al.* (2008). Specimens were examined using Zeiss dissecting microscopes. Photographs were acquired on a BK Plus Lab System featuring a P-51 Cam lift, Optics K2 Long Distance Microscope, and Helicon Focus software. All material is sourced from the Australian National Insect Collection at CSIRO Ecosystem Sciences, Canberra ACT, unless otherwise stated. Collection localities are displayed in Figure 1.

A list of abbreviations is as follows:

AM	Australian Museum, Sydney, Australia
ANIC	Australian National Insect Collection, CSIRO Ecosystem Sciences, Canberra, Australia
GDCD	Greg Daniels Private Collection, Brisbane, Australia
Qld	Queensland
QM	Queensland Museum, Brisbane, Australia
WA	Western Australia
WAM	Western Australian Museum, Perth, Australia

Results

Taxonomy

Subgenus *MYIOSCAPTIA* Mackerras, 1955

Scaptia Walker 1850, subgenus *Myioscaptia* Mackerras, 1955a, fig. 30, p. 496. Type species *Pangonia violacea* Macquart, 1850, Australia, by original designation. Daniels (1989, 2011); Fairchild and Mackerras (1977); Mackerras (1955, p. 496, 1960, p. 122).

Genotype: *Pangonia violacea* Macquart, 1850, Australia, by original designation of Mackerras (1955, p. 496).

Morphological diagnosis. Small (8–11 mm), rotund, blowfly mimicking species, usually bright metallic green to dull semi-metallic black in appearance, differentiated from the other subgenera of *Scaptia* by the short rounded and leaf-like palpi, clear wings and abdomen and scutum without distinct markings.

Female. Length 8–11 mm. Frons usually parallel, sometimes only slightly diverging dorsally and ventrally, narrow, slightly raised at centre. Face truncate to moderately bulging above, with depressions at base and sides, occasionally somewhat shining. Antennal scape and pedicel small, equal to width of stout, cylindrical flagellum with eight distinct flagellomeres, without projections. Palpi short, usually less than length of flagellum and less than one third the length of the proboscis shaft, flattened, broad to resemble the blade of a leaf, with a well defined flat bare area. Proboscis relatively small, less than one and a quarter times head height, relatively slender, heavily chitonised, usually with well-developed labella that is usually greater than the width of the proboscis. Scutum metallic or non-metallic, sometimes shining, usually without conspicuous vittae rarely exceeding the transverse suture. Abdomen short and rotund, metallic or non-metallic, sometimes shining, without obvious markings. Wings clear with prominent stigma; cell *R*5 narrowed, or closed with a short petiole; cell *M*3 open; vein *M*1 without inflexion; *R*4 angulate, with or without appendix (Mackerras 1955, 1960). Mackerras (1960, p. 122) described the genitalia as "eight sternite with gonopophyses rounded; cerci rounded apically; lateral arms of furca relatively large, narrowly fused with lateral edge of 9th tergite.

Male. Length 8–10 mm. Eyes holoptic, with upper facets slightly enlarged. Palpi short, slender, cylindrical and blunt, with an obvious apical lateral bare area. Mackerras (1960, p. 122) described the genitalia as "hypopygium with aedeagus unusually long; coxites normal; style hooked and pointed at tip, but not unusually wide, and without strong hairs.

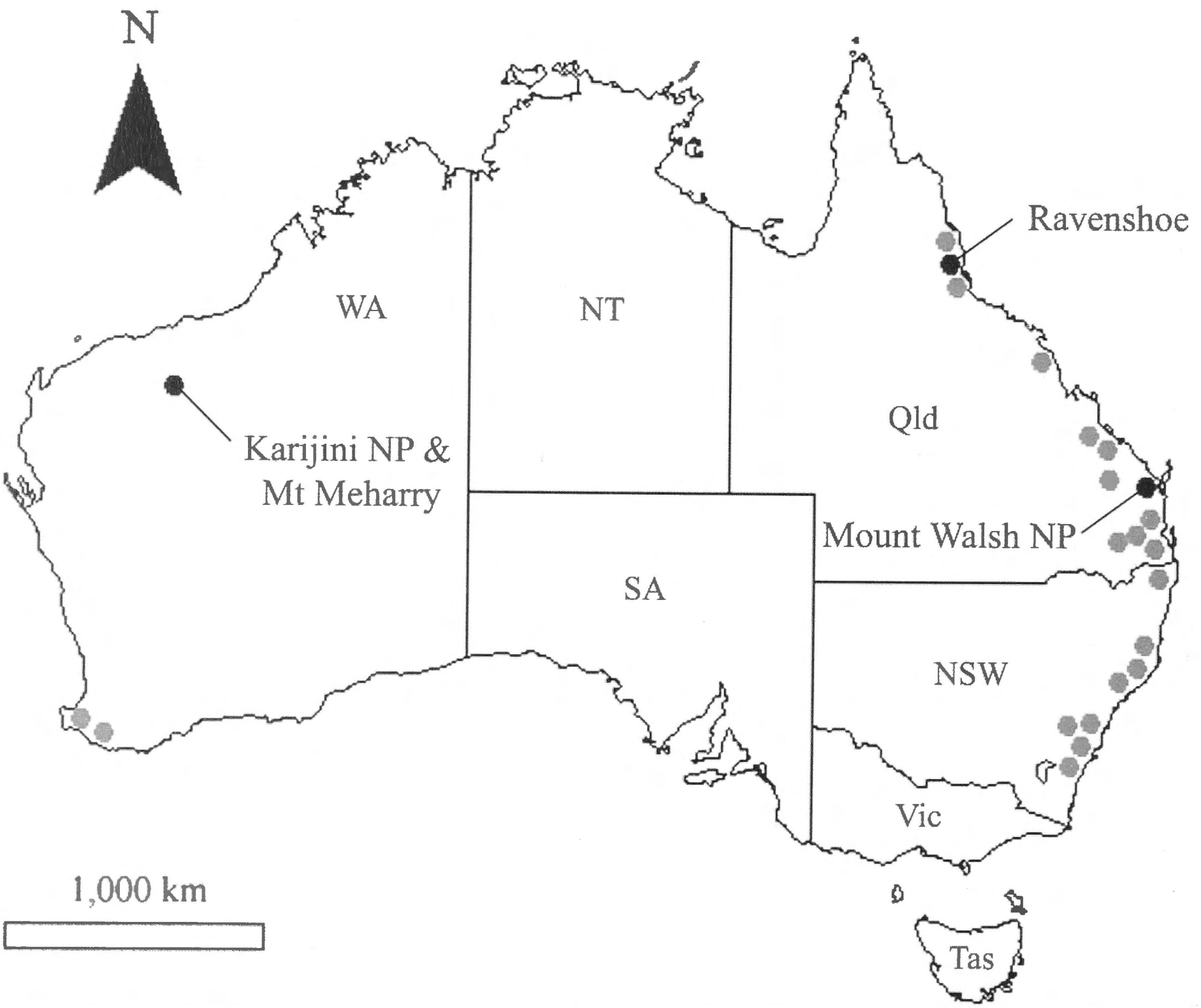

FIGURE 1. The distribution of *Scaptia* (*Myioscaptia*) Mackerras, 1955 and *Scaptia* (*Scaptia*) Walker, 1850 species described in this paper, noting the first records of *Scaptia* (*Myioscaptia*) from inland Western Australia. Black locations represent new collection records for the novel species; grey represent previous collection records for the subgenus *S.* (*Myioscaptia*).

Key to females of Australian species of *Scaptia* (*Myioscaptia*)

1. Dark, green to purplish or blackish species, with abdominal tergites metallic or semi-metallic, and usually a strong resemblance to certain blowflies. 2
- Light grey to yellowish brown species, with at most apical tergites of abdomen shining 10
2. Thorax and abdomen, including venter, bright metallic green to dark purplish blue 3
- Scutum more or less covered with tomentum; abdomen usually dark and dull, venter non-metallic 5
3. Scutum black; abdomen with first two tergites orange brown, contrasting with apical black tergites . . . . . *ferromontana* Daniels, 2011
- Scutum and abdomen concolorous blueish green to purple 4
4. Mesonotum with greyish pruinose stripes; anepisternum dull greyish, less metallic; hairs on margin of calyptral fold whitish. . . . . *violacea* (Macquart, 1850)
- Mesonotum otherwise; more brilliantly metallic, anepisternum metallic, shining; hairs on margins of calyptral fold black . . . . . *inopinata* Fairchild & Mackerras, 1977
5. A black species; abdominal tergites with apical bands of ashy hairs; legs brownish black. North Queensland . . . . . *nigrocincta* Mackerras, 1960
- Beard and pleural hairs creamy to deep gold; abdomen purplish blue to bronzy green or greenish black, with golden hairs, which are densest towards apex 6
6. Cell *R*5 open, or at most closed near wing margin without well-defined petiole; vein *R*4 with at most rudimentary appendix; palpi and legs bright yellowish brown 7
- Cell *R*5 closed, with well-defined petiole; vein *R*4 with strong appendix; palpi and legs brown to dark brown 8
7. Palpi long and narrow; basal flagellomeres swollen; abdomen without blueish hues and less hairy overall; legs with coxae hairs mixed black and gold, femora hairs dark brown to black . . . . . *collessi* Lessard **sp.n.**
- Palpi usually short, wide and rotund, sometimes narrower in northern species; basal flagellomeres cylindrical; abdomen with blueish hues, sometimes dark green to rich purple; leg hairs creamy gold on coxae and predominantly yellow on femora . . . . . *bancrofti* (Austen, 1912)
8. Frons parallel with dark brown and creamy yellow hairs; palpi dark brown, concave laterally, slightly pointed; flagellum reddish brown basally, with terminal three flagellomeres brownish black, sharply contrasting. Eastern Australia . . . . . *calliphora* Mackerras, 1960
- Frons more divergent with entirely dark brown hairs; palpi brown, short and rounded; flagellum more uniform orange to reddish brown. Western Australia 9
9. Flagellum pale orange to reddish brown; palpi almost flat laterally; scutal vittae usually extending beyond transverse suture; legs dark brown; apical hairs on abdomen relatively dense . . . . . *gibbula* (Walker, 1848)
- Flagellum bright orangey brown; palpi with lateral concavity; scutal vittae limited to the front of transverse suture only; legs entirely black; apical hairs on abdomen sparse . . . . . *lambkinae* Lessard **sp.n.**
10. A uniformly light grey species; scutum and abdomen more or less covered with yellowish cream hair. . . . . *muscula* English, 1955
- A yellowish brown species; scutum and anterior half of abdomen more or less covered with tomentum and dull golden hairs; posterior half of abdomen shining dark brown to black.. . . . . *nigroapicalis* Mackerras, 1960

New species

Scaptia (*Myioscaptia*) *collessi* Lessard, sp.n.

(Fig. 2)

Type material. Holotype female, Qld, 18 km north of Ravenshoe near The Craters, 28 Nov 1981, D. H. Colless (AM).

Diagnosis. A small (length 8 mm) *Calliphora*-like species, closely related to the Northern form of *Scaptia* (*Myioscaptia*) *bancrofti* (Austen, 1912), but distinguished as having longer, narrower palpi, flagellomeres swollen at base and tapering towards tip, abdomen less tomentose, with dark brown to black tergites without blueish hues, coxae with mixed black and gold hairs, and femora with dark brown to black hairs.

Female. Length 8mm. **Head.** Eyes with pale brown hairs. Frons parallel, index 2.5, brownish grey with grey zones along margins, hairs dark brown to black; ocellar tubercle raised, dark brown to greyish with long dark brown hairs. Subcallus greyish fawn with a slight yellowish hue, lighter at base of antennae; parafacials greyish fawn, and with brown hairs at lower margins; face yellowish brown to greyish fawn with widened rows of dark brown hairs below each antennae. **Antennae.** 1st and 2nd segment greyish fawn with black hairs; 3rd yellowish brown with basal three flagellomeres swollen, remainder of flagellomeres conspicuously tapering at tip and darkening on apical two, contrasting. **Palpi.** 1st segment yellowish brown with dense brown hairs; 2nd flat,

relatively long, length twice as long as it is wide, obviously tapered, and with sparse pale yellow marginal hairs. Beard dull pale yellow to brown.

Thorax. Scutum and scutellum grey to light slate blue, shining, with pale grey median, dorsocentral lines, transverse suture and lateral margins, hairs on disc black, supra- and postalar tufts mixed black and cream to gold. Pleura greyish brown, darkening below, hairs gold on pronotum and dense on upper anepisternum, dense gold on laterotergite, and with occasional mixed brown hairs on above posteriorly, remainder of hairs predominantly black with some shorter golden hairs on katepisternum.

Legs. Coxae grey to yellowish brown, and with gold hairs dorsally and black ventrally; tarsi and tarsomeres slightly darker than yellow femora, hairs predominantly black, with the exception of the hind femora with sparse golden hairs.

Wings. Grey, somewhat yellowish towards costal cell and basal cells; stigma inconspicuous yellowish brown; veins yellowish brown; *R4* sinuous and with very short appendix; cell *R5* widely open.

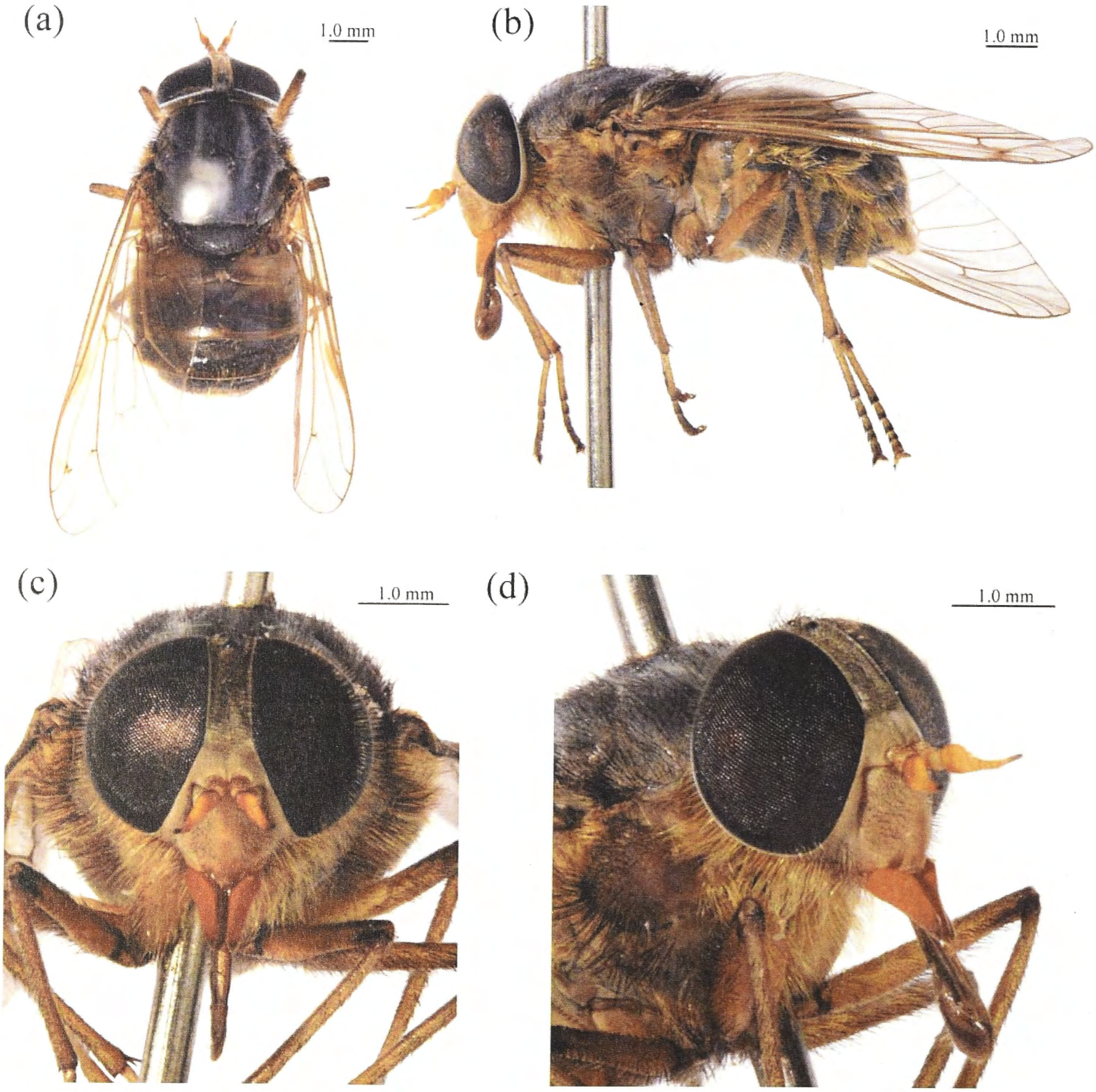

FIGURE 2. *Scaptia* (*Myioscaptia*) *collessi* Lessard, **sp.n.** Holotype female: (a) dorsum; (b) side; (c) front; (d) profile.

Abdomen. Shining, semi-metallic black, and with first tergite brown, remainder black with bronze to golden brown apical bands; hairs on disc golden, black on first tergite with small medial tuft of mixed black and golden hairs, remainder of tergites with dense golden hairs at lateral margins. **Venter.** Shiny, all sternites black with golden apical bands, hairs short and golden.

Remarks. The collection label declares that this specimen was caught "at light". Nothing further is known regarding the species behaviour. This species is closely related to *Scaptia* (*Myioscaptia*) *bancrofti* but notably differs from either form to warrant recognition as a new species.

Distribution. Known only from the holotype locality of north eastern Queensland (Fig. 1).

Etymology. This specific epithet is in honour of the late Don Colless, research scientist and curator of Diptera in the Australian National Insect Collection (ANIC) from 1960 until 1987, and associated with the collection as an Honorary Fellow until 2012. Don Colless collected the only known specimen of this species.

***Scaptia* (*Myioscaptia*) *lambkinae* Lessard, sp.n.**
(Fig. 3)

Type material. Holotype female (1), WA, Karijini National Park, Juna Downs Road, Callitris Gorge, 3 km W of Mt Mossenson, at light, 22°48'S 118°26'E (GPS), 18 May 2003, K. Pullen & A. Zwick (ANIC). Paratype female (1), WA, Mount Meharry summit, hand net, 22°58'50"S 118°35'18"E (GPS), 1257 m, 19 May 2003, C. Lambkin, D. Yeates & J. Recsei (ANIC). Paratype female (1), WA, Pyramid Hill summit, hand net, 21°35'41"S 117°33'00"E (GPS), 229 m, 10 May 2003, C. Lambkin, D. Yeates & J. Recsei (ANIC). Paratype female (1), WA, Summit of Mt Meharry, 22.59°S 118.35°E, 28 June 1984, R.P. McMillan (WAM #79410).

Diagnosis. A small, dark species superficially similar to *Scaptia* (*Myioscaptia*) *gibbula* (Walker, 1848), but distinguished as being less hairy, with bright orangey brown flagellum, legs entirely black, scutal vittae less obvious, limited to front of transverse suture only, and abdominal tergites with sparser apical fringes of short black hairs. Length 11 mm.

Female: Length 11 mm. **Head.** Eyes with dense brown hairs. Frons parallel, slightly diverging, index 2, black with dark brown hairs; ocellar tubercle slightly raised, black. Subcallus dark brown to black, shiny; parafacials black with yellow hairs, becoming brownish towards lower margins; face dark brown to black, shiny with dark brown hairs on each side below antennae. **Antennae.** 1st and 2nd segments dark brown to black with long black hairs; 3rd segment dark orangey brown, darkening on apical flagellomere. **Palpi.** 1st segment black, with dense golden yellow hairs; 2nd segment brown, short, rounded and slightly pointed apically, with lateral concavity and very short brown hairs at margins. Beard golden yellow.

Thorax. Scutum and scutellum dark greyish black, shining, without obvious median and dorsocentral lines or lateral margins; hairs on disc grey to dull yellow; scutellum, supra- and postalar tufts conspicuous, mostly dull yellow, occasionally mixed with brown hairs. Pleura dark brown to black, hairs predominately golden yellow, except for anepisternal and katepisternal tufts mixed with dark brown to black.

Legs. Coxa and femora black, tibiae and tarsomeres dark brown, knees pale yellowish brown; hairs on coxa long, mixed dull yellow and brown, long dull yellow on femora, short dense brown on tibiae and tarsomeres.

Wings. Grey, more yellowish and brown towards apical basal cells; stigma brown, subtle; veins brown; *R*4 with short appendix; cell *R*5 closed on wing margin.

Abdomen. Shining metallic black, unbanded; disc hairs black, with dense golden yellow hairs towards lateral margins of all tergites, hairs black on apical tergite. **Venter.** Shining black; hairs dense, predominantly golden yellow.

Distribution. Inland central west Western Australia (Fig. 1). This species further extends the known distribution of the subgenus over 700 km NE into central of Western Australia.

Etymology. This specific epithet is in honour of Dr Christine Lambkin who collected several specimens of the species and for consistently providing material for examination.

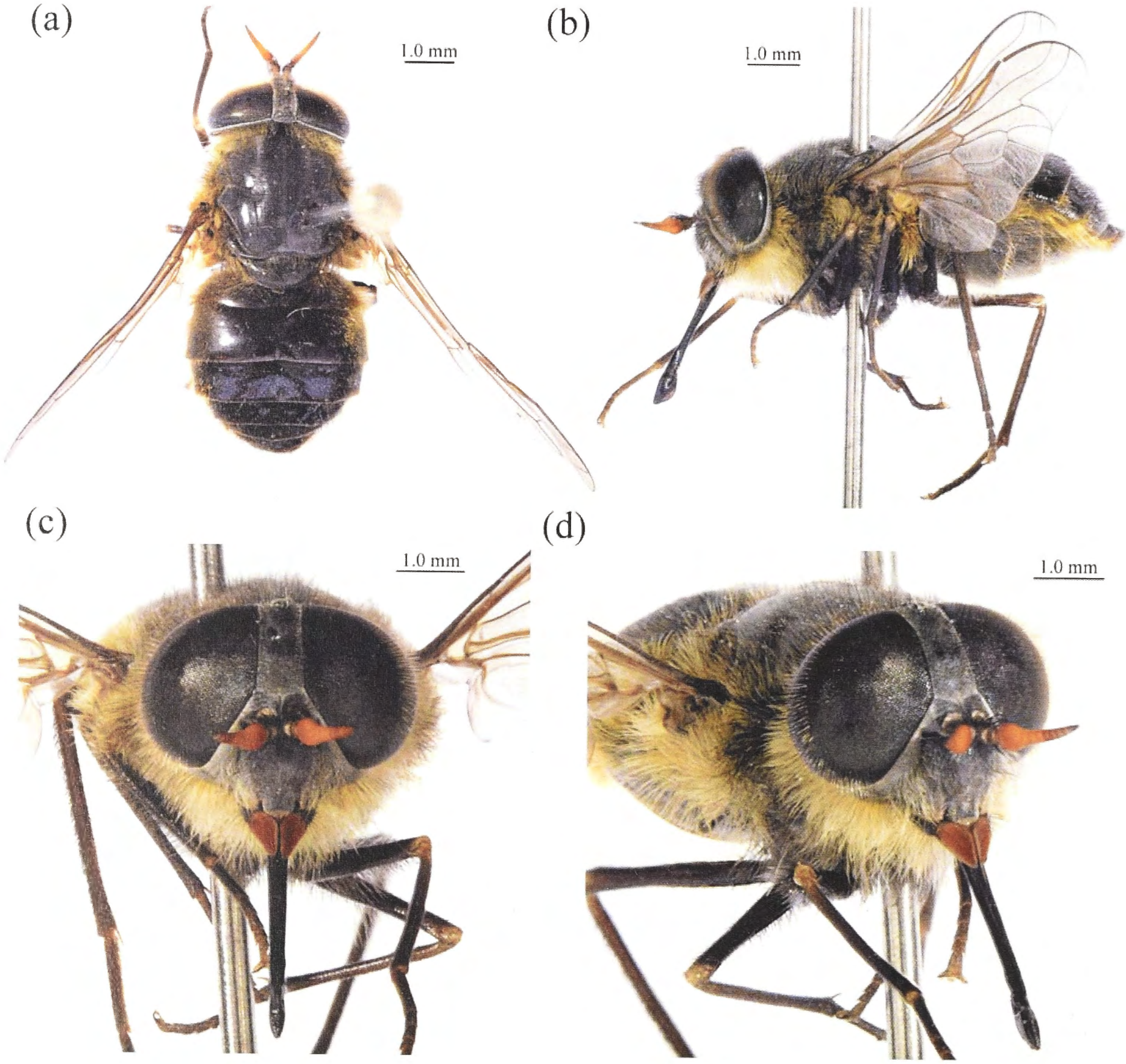

FIGURE 3. *Scaptia* (*Myioscaptia*) *lambkinae* Lessard, **sp.n.** Holotype female: (a) dorsum; (b) side; (c) front; (d) profile.

Subgenus *SCAPTIA* Walker, 1850

Scaptia Walker, 1850. Type species *Pangonia aurata* Macquart, 1838, Australia, by designation of Coquillett (1910, p. 603). Ferguson (1924, 1926).
Scaptia Walker, 1850, subgenus *Scaptia* Mackerras 1955, p. 490. Daniels (1989); Mackerras (1960, p. 36).

Genotype: *Pangonia aurata* Macquart, 1838, Australia, by designation of Coquillett (1910, p. 603).

Morphological diagnosis. Mostly solidly built species, with relatively short and strong legs. Distinguished from other subgenera by the parallel frons, large and pointed sabre-like palpi, and short, thick proboscis with large well-developed labella.

Female. Length 7–18 mm. Frons narrow, usually parallel or slightly converging at base (index usually 2.0 to 4.0), slightly raised at centre for some species, subcallus occasionally bulging and distinct. Face truncate, with depressions at base and sides, without obviously shining. Antennal scape and pedicel small, almost equal to length of flagellum with eight distinct flagellomeres, widest on first basal segment before tapering at tip, without

projections. Palpi long, usually equal or greater than the length of the flagellum and greater than half the length of the proboscis shaft, sometimes only shorter the flagellum length or than half the length of the proboscis shaft, usually laterally compressed, pointed and sabre-like, and a conspicuously broad lateral bare area. Proboscis short, usually as long as the height of the head, thick and heavily chitonised, with large, well-developed labella greater than the width of the proboscis. Scutum with or without conspicuous vittae, occasionally exceeding transverse suture. Abdomen usually stout and rotund, with or without obvious markings or patterns. Wing usually clear, occasionally spotted at crossveins or with radial suffusion; stigma mostly inconspicuous; cell *R*5 usually open, sometimes narrowed, rarely closed; cell *M*3 open; vein *M*1 without inflexion; *R*4 angulate, with or without appendix (Mackerras 1955, 1960). Mackerras (1960, p. 36) described the genitalia as having the "eighth sternite with gonopohyses often rounded; cerci often truncate apically; lateral arms of furca not fused with 9th tergite.

Male. Length 7–15 mm. Eyes holoptic, with upper facets slightly enlarged. Palpi short and slender, cylindrical, blunt at tip, and with an apical lateral bare area. Mackerras (1960, p. 36) described the genitalia as having the "style of hypopygium finger-like, rounded at tip.

New species

Scaptia (*Scaptia*) *aurinigra* Lessard, sp.n.

(Figs. 4 & 5)

Type material. Holotype female, Qld, Rockpool Gorge, Mount Walsh National Park, Biggenden, 4 Oct., 1976, H. Frauca (ANIC). Paratype male same data as for Holotype (ANIC).

Diagnosis. A small, dark, muscoid-like species superficially resembling *S.* (*Myioscaptia*), but placed within *S.* (*Scaptia*) due to its long sabre-like palpi exceeding half the length of the proboscis shaft, most similar to *Scaptia* (*Scaptia*) *minuscula* Mackerras, 1960, but distinguished by its scutum without vittae, unbanded abdomen, mostly clear to slightly greyish wings, orange to yellow antennae, and dark brownish black beard and legs. Length 8–9 mm.

Female. Length 9 mm. **Head.** Eyes with short, brown hairs. Frons parallel, index 2.2, dark brown-black, with dull golden fawn around eye margins that meets at median callus, hairs dark brown-black; ocellar tubercle black. Subcallus brownish fawn, becoming darker towards base of antennae; parafacials brownish fawn with dark brown hairs at lower margins; face brownish fawn, darker at centre, with short brown hairs on each side below antennae. **Antennae.** Scape and pedicel pale brownish fawn to orange, with black hairs; flagellum bright yellow to orange, concolorous, and tapering at tip with segmentation less conspicuous. Palpi orange to brown; 1st segment with large, black hairs; 2nd segment with distinct pale orange-brown concavity and very short black hairs at margins. Beard dark brown-black.

Thorax. Scutum and scutellum black, with a vague blueish hue, rather shiny, without grey median, dorsocentral and lateral margins lines, hairs on disc entirely black, post-alar tuft predominantly black. Pleura dull greyish brown-black, with hairs entirely black, including propleural, hypopleural and squamal tufts.

Legs. Coxae, femora, tibiae and tarsomeres entirely dark brown to black, concolorous, hairs dark brown, except for pale ventral zone on all tarsi and fore tibiae only.

Wings. Clear to faintly greyish; stigma brown; veins brown; *R*4 angulate, without appendix; cell *R*5 widely open.

Abdomen. Shining metallic black, with a vague blueish hue, becoming slightly duller and greyish towards apical tergites, hairs black on disc and on abdominal margins, without banded appearance, with somewhat lighter at apical margins on tergites. Venter. Black with blusih hues on apical half of sternites, brown on basal half, becoming duller grey from sternites four onwards, with predominantly black hairs.

Male. Length 8 mm. Upper facets of eyes enlarged, hairs very dense, golden brown. Parafacials browner than females, with dense brown hairs. Palpi rod-like, long, slightly pointed with large apical lateral bare area with long brown to black hairs. Apical segments of abdomen shining with a slightly deeper purple to blueish hue than females.

Distribution. Known only from the type locality of south eastern Queensland.

Etymology. This specific epithet is derived from the latin *auri*, gold, and *nigra*, black, referring to the bright yellow antennae which sharply contrast the black scutum, abdomen and legs.

Remarks. This species is keyed out in couplet 11 of Mackerras (1960, p. 39) key to the Australian *S.* (*Scaptia*) species. Furthermore, it may provide a link between *S.* (*Scaptia*) and *S.* (*Myioscaptia*) as it shares the general muscoid-like appearance of the latter subgenus, and only substantially differs in its long sabre-like palpi conserved to *S.* (*Scaptia*) species.

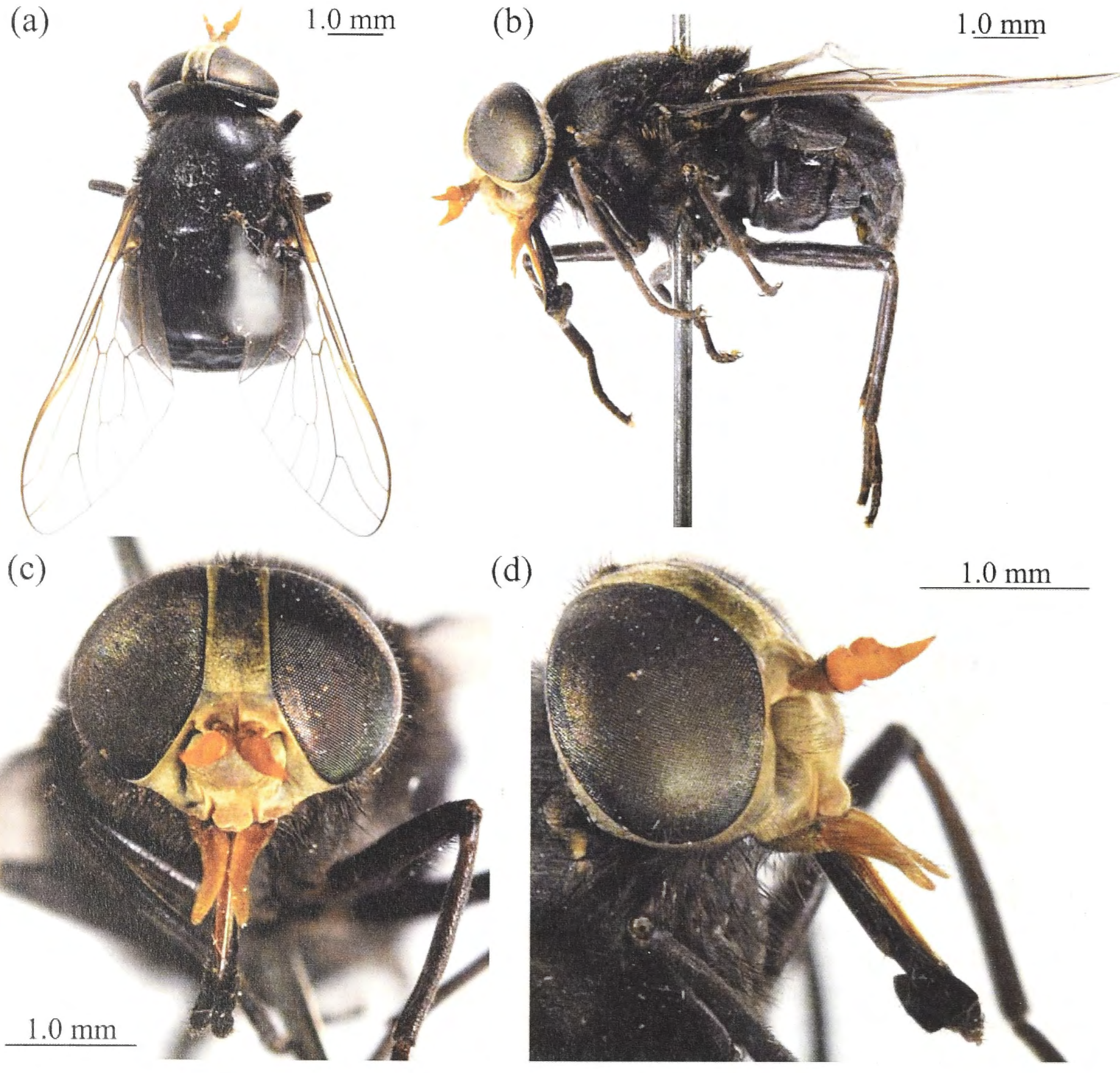

FIGURE 4. *Scaptia* (*Myioscaptia*) *aurinigra* Lessard, **sp.n.** Holotype female: (a) dorsum; (b) side; (c) front; (d) profile.

Addendum

The Holotype of *Scaptia* (*Plinthina*) *nigripuncta* Lessard, 2011 in Lessard and Yeates (2011, p. 250) is in fact lodged within the QM, instead of the ANIC as originally listed. Similarly, the entire set of type material of *Scaptia* (*Pseudoscione*) *casseli* Lessard, 2012 in Lessard and Yeates (2012b, p. 12) will be lodged within the AM, instead of GDCB as originally listed.

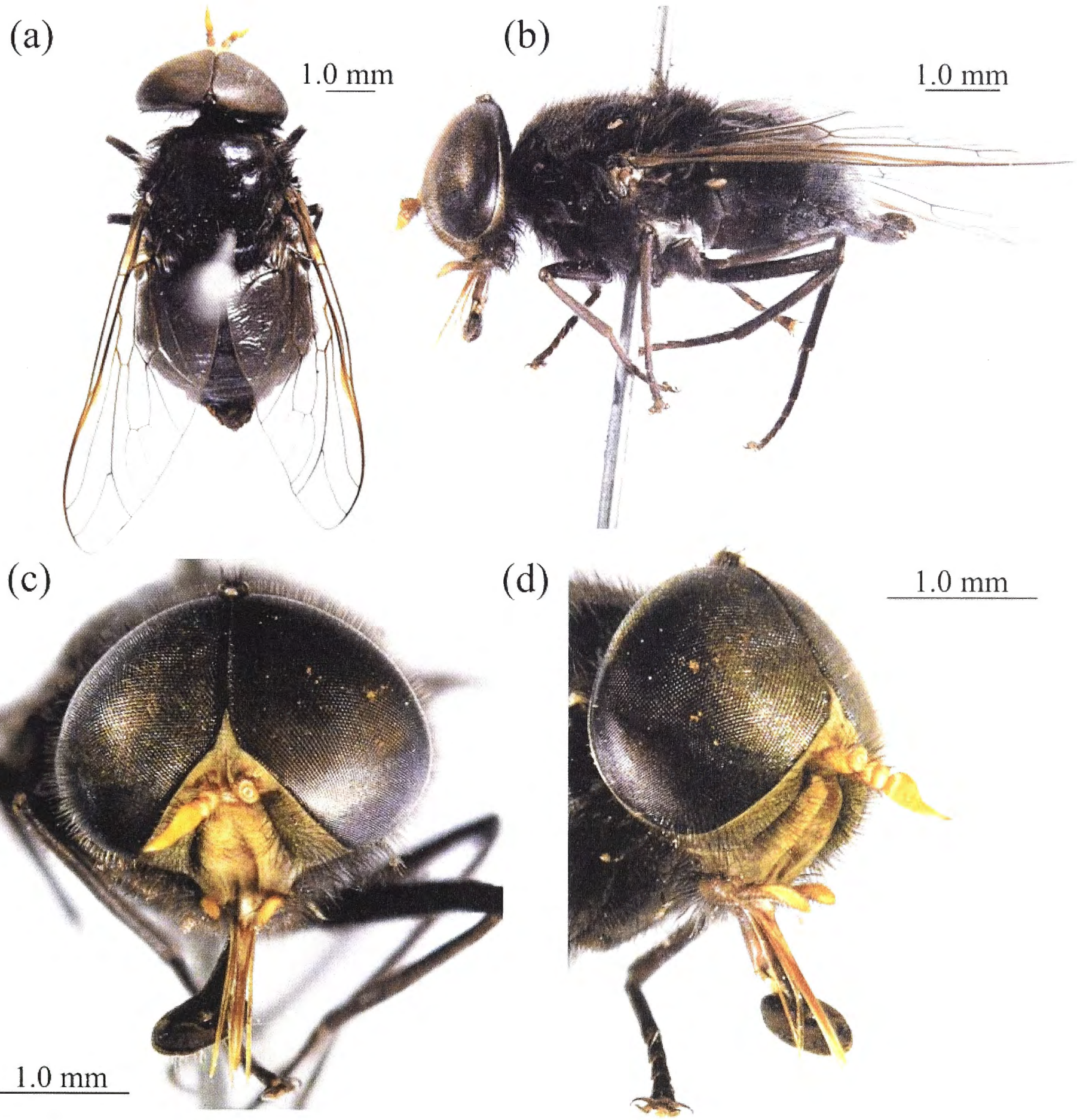

FIGURE 5. *Scaptia* (*Scaptia*) *aurinigra* Lessard, **sp.n.** Holotype male: (a) dorsum; (b) side; (c) front; (d) profile.

Discussion

Several recently described species of *Scaptia* have extended the known distribution of the Scionini into unexpected regions of Australia. These include areas where the tribe was previously though absent or unable to survive, despite some regions having an extensive history of entomological collection. The new species *Scaptia* (*Myioscaptia*) *lambkinae* Lessard, **sp.n.** extends the known distribution of the Scionini over 700 km further NE into central Western Australia where it has not been previously collected. In addition, the species *Scaptia* (*Plinthina*) *arnhemensis* Lessard, 2011 and *Scaptia* (*Plinthina*) *nelsonae* Lessard, 2011 were the first records of the Scionini from the northern coast of central Australia, including northeast of the Northern Territory and Western Australia, respectively (Lessard and Yeates 2011). The most significant extension corresponds to *Scaptia* (*Pseudoscione*) *mackerrasi* Lessard, 2012, collected from Alice Springs in the Northern Territory, and is the only central species of Australian Scionini (Lessard and Yeates 2012b). The nearest recorded species to this was over 700 km NE of Alice

Springs belonging to *S.* (*Pl.*) *arnhemensis* Lessard, 2011 collected from Musselbrooke Creek, Lawn Hill National Park, Queensland. Moreover, *S.* (*Ps.*) *mackerrasi* Lessard, 2012 is located over 1200 km NW from the nearest species recorded from within the same subgenus, *Scaptia* (*Pseudoscione*) *guttipennis* (Ferguson, 1924), Cleve, South Australia.

The Australian Scionini were previously considered to be limited to mild-temperate to subtropical environments, as the majority of species are restricted to the Australian coast (Mackerras 1960). Temperature and availability of soil moisture were further thought to restrict the distribution of the tribe, both regulating breeding behaviour, larval development in soil or plant substrate, frequency of adult emergence, and sustainability of flowers for feeding (Mackerras 1960). The recently described species, in particular *S.* (*Ps.*) *mackerrasi* Lessard, 2012 and *S.* (*M.*) *lambkinae* Lessard, **sp.n.**, are the first records of the Scionini to occur in inland Australia. Both species were collected within close proximity to gorges, presumably surviving desiccation by taking advantage of cooler temperatures during the day and an increase in water availability for larval development. Based on these collection records, the Scionini appear to be adapted to tolerate and persist in dry, drought prone regions of Australia that are often subjected to extreme temperatures. Therefore, additional Scionini species are expected to occur in more remote arid regions of Australia.

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Afterword: Chapters Three to Six

Traditional morphological characters were useful in diagnosing and describing 18 novel species of Australian and New Zealand Scionini presented in Chapters Three to Six. These included five novel species of *Scaptia* (*Plinthina*) (Chapter Three), three novel species of the novel genus *Anzomyia* Lessard, 2012 (Chapter Four), seven novel species of *Scaptia* (*Pseudoscione*) (Chapter Five), two new species of *Scaptia* (*Myioscaptia*) and one new species of *Scaptia* (*Scaptia*) (Chapter Six). Not only were these new species described and illustrated, the new taxa were also included in the updated taxonomic keys to species for the respective genera and subgenera. The amended taxonomic keys now include all the known species of the Australian and New Zealand Scionini. This will ultimately aid in the subsequent morphological identifications of species collected for the large molecular analyses assessing the phylogenetic relationships and biogeography of the Scionini (Chapter Seven). Furthermore, the newly described species can now be incorporated into the formal taxonomic revision of the tribe (Chapter Eight).

Chapter Seven

The evolution and biogeography of the austral horse fly tribe Scionini (Diptera: Tabanidae: Pangoniinae) inferred from multiple mitochondrial and nuclear genes

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The evolution and biogeography of the austral horse fly tribe Scionini (Diptera: Tabanidae: Pangoniinae) inferred from multiple mitochondrial and nuclear genes

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ABSTRACT

Phylogenetic relationships within the Tabanidae are largely unknown, despite their considerable medical and ecological importance. The first robust phylogenetic hypothesis for the horse fly tribe Scionini is provided, completing the systematic placement of all tribes in the subfamily Pangoniinae. The Scionini consists of seven mostly southern hemisphere genera distributed in Australia, New Guinea, New Zealand and South America. A 5757 bp alignment of 6 genes, including mitochondrial (COI and COII), ribosomal (28S) and nuclear (AATS and CAD regions 1, 3 and 4) genes, was analysed for 176 taxa using both Bayesian and maximum likelihood approaches. Results indicate the Scionini are strongly monophyletic, with the exclusion of the only northern hemisphere genus *Goniops*. The South American genera *Fidena*, *Pityocera* and *Scione* were strongly monophyletic, corresponding to current morphology-based classification schemes. The most widespread genus *Scaptia* was paraphyletic and formed nine strongly supported monophyletic clades, each corresponding to either the current subgenera or several previously synonymised genera that should be formally resurrected. Molecular results also reveal a newly recognised genus endemic to New Zealand, formerly placed within *Scaptia*. Divergence time estimation was employed to assess the global biogeographical patterns in the Pangoniinae. These analyses demonstrated that the Scionini are a typical Gondwanan group whose diversification was influenced by the fragmentation of that ancient land mass. Furthermore, results indicate that the Scionini most likely originated in Australia and subsequently radiated to New Zealand and South American by both long distance dispersal and vicariance. The phylogenetic framework of the Scionini provided herein will be valuable for taxonomic revisions of the Tabanidae.

1. Introduction

The Tabanidae, commonly referred to as horse, deer or march flies, are a large cosmopolitan Dipteran family with nearly 4400 described species (Pape and Thompson, 2012). The family exhibits sexual dimorphism in feeding habits, as adult females are typically blood-feeding, whereas males are nectar feeding. Consequently, female horse flies are principal vectors of many disease-causing microorganisms accumulated in the mouthparts, salivary glands and/or tarsi that are mechanically transferred during feeding. Horse flies spread anaplasmosis (Scoles et al., 2008) and bovine leukaemia virus (Foil et al., 1988) in cattle, equine infectious anaemia in horses (Foil et al., 1984), and the filarial nematode *Pelecitus roemeri* and trypanosomiases (Reid et al., 2001) in kangaroos and wallabies (Spratt, 1972a,b, 1974a,b, 1975). Humans can also be affected by the feeding habits of females, including infections of loiasis, tularaemia and even anthrax (Krinsky, 1976; Foil, 1989).

In contrast, nectar-feeding by adult horse flies reinforces the ecological importance of the family as vital pollinators (Johnson and Morita, 2006; Lessard and Yeates, 2012b; Mackerras, 1957, 1960). Myrtaceae are commonly frequented by horse flies in the southern hemisphere, including *Eucalyptus*, *Grevillea* and *Melaleuca* in Australia, *Leptospermum* in both Australia and New Zealand, and *Luma* in South America (Lessard and Yeates, 2012b; Mackerras, 1957, 1960; Tillyard, 1926).

The taxonomy of the Tabanidae is fairly stable as a result of the extensive work of Mackerras (1954, 1955) who provided a classification scheme that is still in use today. This scheme is based on external and genital characters of adults and includes four subfamilies, with further division into one to four tribes: Chrysopsinae

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(Bouvieromyiini, Chrysopini and Rhinomyzini), Pangoniinae (Mycteromyiini [added by Coscarón and Philip (1979)], Pangoniini, Philolichini and Scionini), Scepsidinae, and the largest of the subfamilies Tabaninae (Diachlorini, Haematopotini and Tabanini).

The subfamily Pangoniinae has a near global distribution, with members usually possessing a long proboscis and relatively long, slender legs that are well adapted to grasping flowers (Mackerras, 1955). Currently the Pangoniinae consists of four tribes: the Mycteromyiini (Neotropical in distribution), Pangoniini (Australasian, Nearctic, Neotropical and Palearctic), Philolichini (Afrotropical, Australasian and Oriental) and the Scionini (Australasian, Nearctic and Neotropical) (Coscarón and Philip, 1979; Lessard and Yeates, 2011, 2012a,b; Mackerras, 1954, 1955; Morita, 2008).

The Scionini are mostly stout, bearded and hairy-eyed flies. The tribe is currently divided into seven genera, of which some are further divided into subgenera (Fig. 1): *Anzomyia* Lessard, 2012, *Caenopangonia* Kröber, 1930, *Fidena* Walker, 1850, *Goniops* Aldrich, 1892, *Pityocera* Giglio-Tos, 1896, *Scaptia* Walker, 1850, and *Scione* Walker, 1850. The tribe occurs predominantly in the southern hemisphere (Coscarón and Wilkerson, 1985; Coscarón and González, 2001; Coscarón and Iide, 2003; Lessard and Yeates, 2011, 2012a,b; Mackerras, 1957, 1960, 1961, 1964; Oldroyd, 1947; Wilkerson and Coscarón, 1984), with the exception of the monotypic genus *Goniops* that is endemic to the Nearctic. The two peculiar genera, *Caenopangonia* and *Goniops*, notably differ from the remainder of Scionini by possessing bare eyes and an extremely widened frons.

The genus *Scaptia* is the most species-rich of all the Scionini and has an exclusive southern hemisphere distribution in Australia, New Guinea, New Zealand and South America. The genus is further

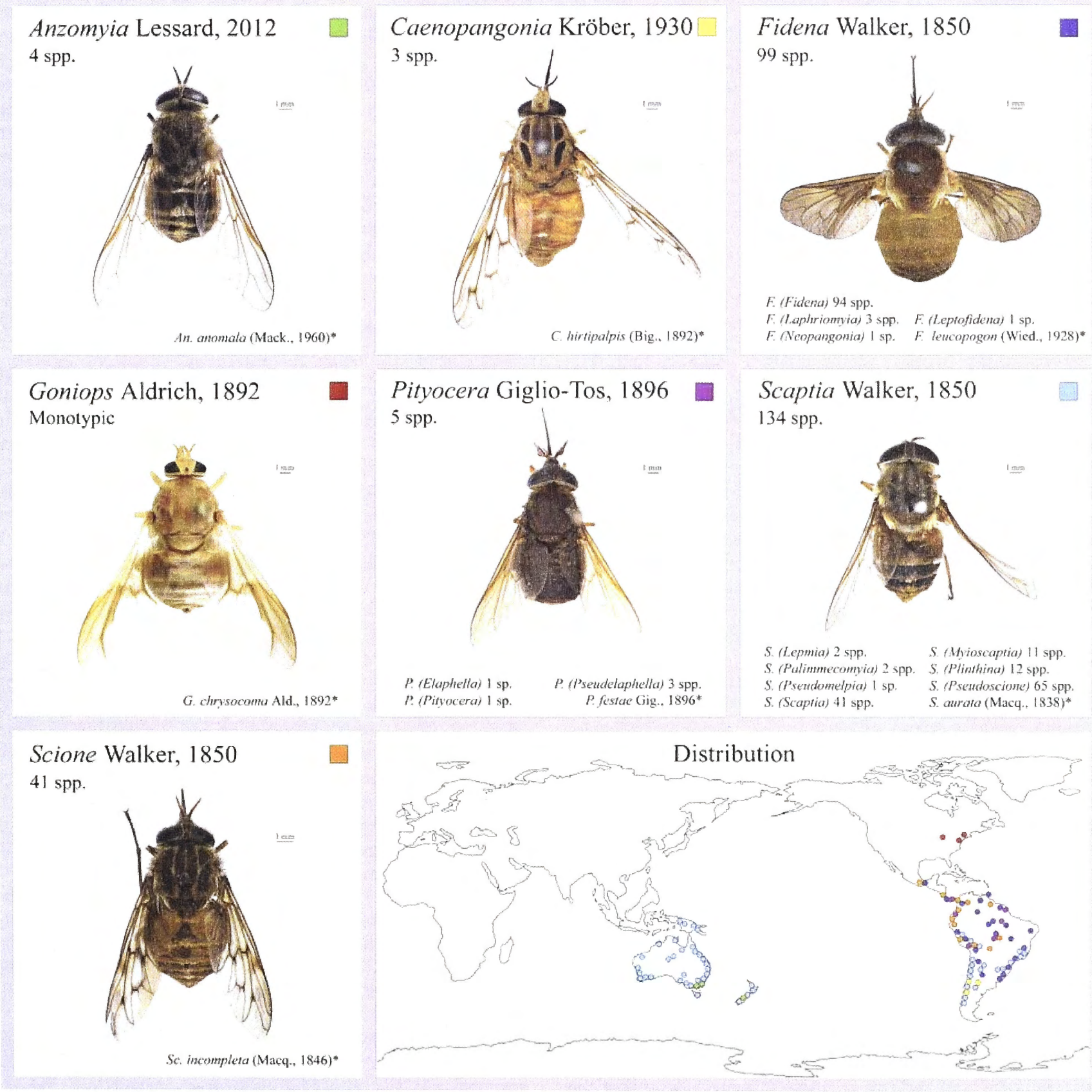

Fig. 1. The genera and distribution of the Scionini, including subgenera and species richness. All type species are illustrated, with the exception of *Caenopangonia brevirostris* (Philippi, 1865).

Chapter Seven

divided into seven subgenera (Fig. 1), including *Lepmia* Fairchild 1969 (found in Brazil), *Pseudomelpia* Enderlein, 1922 (Chile), *Myioscaptia* Mackerras, 1955 (Australia), *Palimmecomyia* Taylor 1917 (Australia), *Plinthina* Walker, 1850 (Australia), *Scaptia* Walker, 1850 (Australia, Chile, Peru, Bolivia, Argentina) and *Pseudoscione* Lutz in Lutz, Araujo and Fonseca 1918 (Australia, Argentina, Brazil, Chile, New Guinea and New Zealand).

The taxonomy of the family below the tribal level is challenging and the phylogenetic relationships are largely unknown. The identification and classification is hindered by the typical lack of definitive characters for genera and species, particularly demonstrated in the genitalia where large structural differences do not correspond with differences in external morphology, which often cannot aid in species identification (Mackerras, 1955, 1960). Preservation can also impact on common diagnostic characters, such as the augmentation of proboscis length during death (Wilkerson and Coscarón, 1984), which can impede subgeneric diagnoses, or colour fading that can affect species-level identification of specimens (Mackerras, 1960; Mackerras et al., 2008).

Modern workers have found strong support for the monophyly for the Tabanidae, based on both morphological (Mackerras, 1954; Yeates, 2002) and molecular evidence (Morita, 2008; Wiegmann et al., 2000, 2003, 2011). Molecular data has been recently successful in reconstructing phylogenetic histories for the Tabanidae. Wiegmann et al. (2000) used the ribosomal 28S gene to demonstrate the well-supported monophyly of the Tabanidae, with each major subfamily recovering as monophyletic, including two species of the Chrysopsinae, four species of the Tabaninae, and two species of the Pangoniinae, each belonging to the Mycteromyiini and Pangoniini (Wiegmann et al., 2000; Fig. 2, p. 1035). Morita (2008) was the first to explore the phylogenetic relationships of the Tabanidae below the subfamily level using Cytochrome Oxidase Subunit One (COI) and the first fragment of the nuclear protein-coding gene carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD1; Moulton and Wiegmann, 2004). This previous study demonstrated strong support for the monophyly of each subfamily, however, focused only on the tribes Pangoniini and Philolichini from the subfamily Pangoniinae and did not include members of the tribe Scionini. Other studies on the systematics of the Tabanidae remain extremely limited.

The phylogeny and taxonomy of the Scionini is thus unclear and hindered by the limited availability of reliable morphological characters. Moreover, the original descriptions for many genera are frequently insufficient and provided with little systematic context, with many genera often presented without a formal description or solely mentioned in either a taxonomic key or checklist of species (Enderlein, 1922, 1925; Lutz et al., 1918). The present study employs molecular data to provide the first robust quantitative phylogenetic framework and insight into the evolution of the Scionini, with a focus on the widely dispersed genus *Scaptia*. It extends the work of Morita (2008) by testing the utility of current morphological classification schemes within the Tabanidae. Divergence time estimation and the fossil record is used to determine whether the current distribution of the Scionini is a result of the sequential fragmentation of the ancient supercontinent of Gondwana, as well as providing insights into the origin of the tribe.

2. Materials and methods

2.1. Taxon sampling

Scionini specimens were collected from a range of localities in Australia, New Zealand and the Americas (Table 1). Six out of the seven Scionini genera were sampled, including the monotypic *Goniops*, four species of *Fidena*, one species of *Pityocera*, 7 species of *Scione*, one species of *Anzomyia*, and for the subgenera of *Scaptia*, three species of *Scaptia* (*Myioscaptia*), four species of *Scaptia* (*Plinthina*), 27 species of *Scaptia* (*Pseudoscione*), and 16 species of *Scaptia* (*Scaptia*). Specimens were identified to species using morphological keys to adults (Coscarón and Wilkerson, 1985; Kröber, 1930a,b, 1933; Lessard and Yeates, 2011, 2012a,b, 2013; Mackerras, 1957, 1960; Wilkerson and Coscarón, 1984) and compared with previously collected material held in the Australian National Insect Collection (ANIC), CSIRO Ecosystem Sciences, Canberra, Australia, the Natural History Museum (NHM), London, UK, the North Carolina State University (NCSU) Insect Collection, Raleigh, USA, and the Smithsonian Institution (SI), Washington DC, USA. Horse fly specimens were preserved in absolute ethanol and stored at -20 °C at either the ANIC or NCSU Diptera collections.

2.2. The fossil Tabanidae

There are currently five recognised compression fossils of the Tabanidae from the Lower Cretaceous, including *Cratotabanus stenomyomorphus* Martins-Neto and Santos, 1994 and *Cratotabanus* sp. Martins-Neto, 2003 (both 121–99 MY; Crato Formation, Brazil; Grimaldi et al., 2011; Martins-Neto, 2003; Martins-Neto and Santos, 1994), *Eopangonius pletus* Ren, 1998 (127–121 MY; Yixian Formation, China; Ren, 1998), *Eotabanoid lordi* Mostovski, Jarzembowski and Coram, 2003 (144–140 MY; Upper Berriasian Durlston Formation, England; Mostovski et al., 2003) and *Laiyangitabanus formosus* Zhang, 2012 (145–140 MY; Late Tithonian, Upper Jurassic to Early Berriasian, Lower Cretaceous; Laiyang Formation, China; Zhang, 2012). Unfortunately, many of these fossils cannot be accurately assigned to a particular subfamily due to the failed preservation of key diagnostic features, such as the hind tibial spurs, antennal flagellum and ocelli (Mostovski et al., 2003; Zhang, 2012).

The fossils originally described by Ren (1998) in the subfamily Pangoniinae have either been criticised as belonging to that subfamily or have been subsequently removed altogether from the Tabanidae. Based on the preserved wing morphology, Grimaldi et al. (2011) identified *Palaepangonius eupterus* Ren, 1998 (127–121 MY; Yixian Formation, China; Ren, 1998) as being inconsistent with the Tabanidae, and the genus was eventually transferred to the Athericidae (Zhang, 2012). Furthermore, *E. pletus* is no longer recognised as a member of the Pangoniinae and cannot be assigned to any subfamily due to the failed preservation of the diagnostic hind tibial spurs and antennal flagellum (Zhang, 2012). Similarly, *Baissomyia redita* Mostovski, Jarzembowski and Coram, 2003 (137–127 MY; Lower Cretaceous; Zaza Formation, Russia; Mostovski et al., 2003), which was provisionally described within the Tabanidae, cannot be confidently placed within the family due to the poor preservation of the wings and is currently recognised as a stem group of the Tabanomorpha (Mostovski et al., 2003). At present, the compression fossils *E. lordi* and *La. formosus*, which span two continents (China and the UK), are considered to be the oldest and most reliable fossils of the Tabanidae based on the almost complete preservation of the wings, confirming the secure placement of these fossils within the family (Mostovski et al., 2003; Zhang, 2012). Therefore, the known ages of these two independent fossils will be valuable for estimating the divergence times of the Tabanidae presented in this study (Section 2.5).

2.3. DNA extraction, amplification and sequencing

Whole genomic DNA was extracted from the flight muscles or legs of adult horse fly specimens with the DNeasy Tissue Kit (Qiagen, Valencia, CA) as per manufacturer's instructions, keeping the voucher specimen for reference. The purified DNA was resuspended in 50 μL of elution buffer and stored at 4 °C.

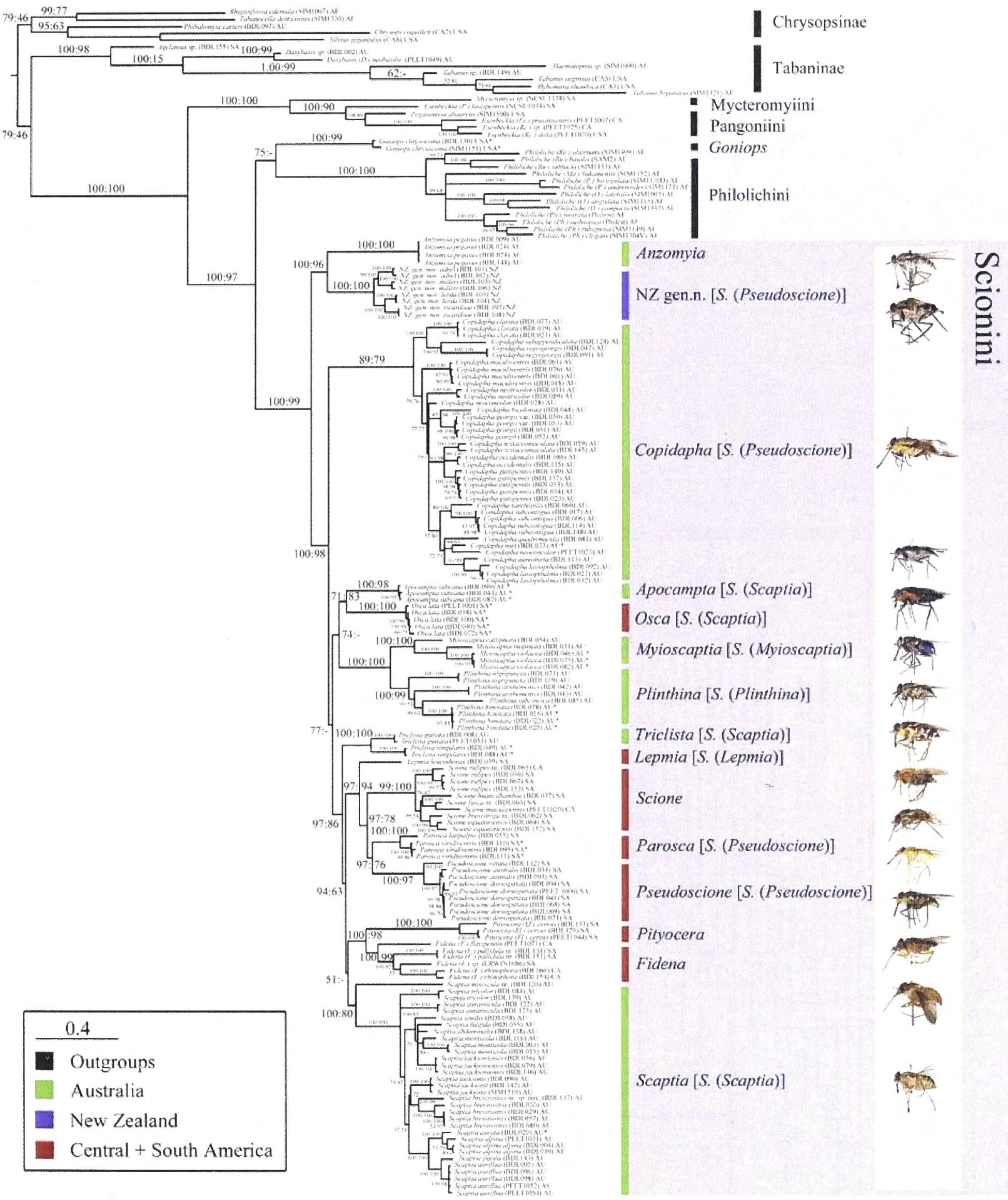

Fig. 2. Molecular phylogeny of the revised Scionini provided by Bayesian (PP = Posterior Probability; GTR + I + G; four chains; 20 M generations) and maximum likelihood (BS = Bootstrap Support) analyses of the combined mitochondrial (COI and COII) and nuclear gene markers (AATS, CAD and 28S). All branch tips have PP values of 100. Names in square parentheses refer to the old classification scheme for the newly revised genera. Tip labels refer to revised taxa. Outgroups have not been colour coded for region. AF, Africa; AU, Australia; CA, Central America; NZ, New Zealand; SA, South America; USA, United States of America.

Multiple fragments of four genes were targeted for amplification and sequencing, chosen to cover a range of genetic mutation rates to maximise phylogenetic signal. The nuclear genes targeted for amplification included ribosomal 28S (869 bp; indels were included), along with the protein coding genes alanyl-tRNA synthetase (AATS, 382 bp) and three distinct regions of CAD (CAD1, 816 bp; CAD3, 758 bp; CAD4, 776 bp) responsible for encoding the first three enzymatic activities of the de novo pyrimidine biosynthetic pathway (Moulton and Wiegmann, 2004). Mitochondrial loci included the first two subunits of the cytochrome oxidase gene, with COI amplified from two separate fragments (COI: COIa, 5′ end, 824 bp; COIb, 3′ end, 639 bp: COII, 693 bp). Primer pairs are presented in Supplementary material (Table S1) (Lui and Beckenbach, 1992; Moulton and Wiegmann, 2004; Simon et al., 1994; Sperling et al., 1994; Whiting, 2002; Wiegmann et al., 2000).

PCRs were performed in either 25 μL reactions using either *TaKaRa Ex Taq*™ Hot Start Version (Takara Bio Inc., Japan) or *Scientifix* Hot Start DNA Polymerase (Scientifix Pty Ltd., Australia)

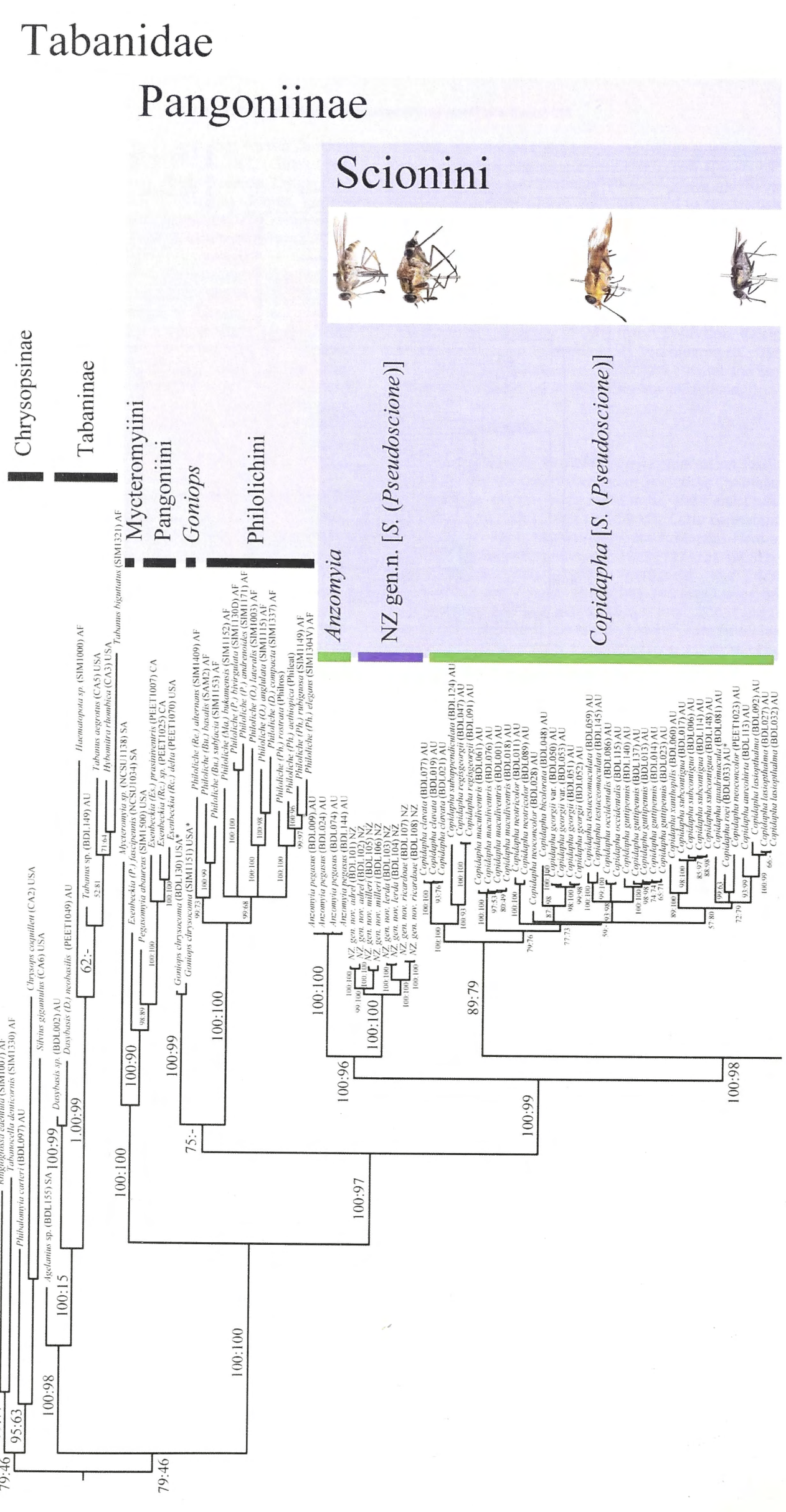
Tabanidae
Pangoniinae
Scionini
Chrysopsinae
Tabaninae
Mycteromyiini
Pangoniini
Goniops
Philolichini
Anzomyia
NZ gen.n. [S. (Pseudoscione)]
Copidapha [S. (Pseudoscione)]
Rhigiogłossa edentula (SIM1007) AF
Tabanocella denticornis (SIM1330) AF
Philadamyia carteri (BDL097) AU
Chrysops coquilleti (CA2) USA
Silvius gigantulus (CA6) USA
Agelanius sp. (BDL155) SA
Dasybasis sp. (BDL002) AU
Dasybasis (D.) neobasilis (PEET1049) AU
Tabanus sp. (BDL149) AU
Tabanus aegrotus (CA5) USA
Hybomitra rhombicca (CA3) USA
Haematopota sp. (SIM1
Tabanus bigantatus (SIM1321) AF
Mycteromyia sp. (NCSU1138) SA
Exeibeckia (P.) fascipennis (NCSU1034) SA
Peggiomyia abaureas (SIM1500) USA
Exeibeckia (Es.) prasiaventris (PEET1007) CA
Exeibeckia (Rc.) sp. (PEET1025) CA
Exeibeckia (Rc.) delta (PEET1070) USA
Goniops chrysocoma (BDL130) USA*
Goniops chrysocoma (SIM1151) USA*
Philoliche (Rc.) alternans (SIM14
Philoliche (Bu.) basalis (SAM2) AF
Philoliche (Bu.) subfacia (SIM1153) AF
Philoliche (Ma.) bukamensis (S
Philoliche (P.) bivirgulata (SIM1152) AF
Philoliche (P.) amdrenoides (SIM1171) AF
Philoliche (O.) lateralis (SIM1003) AF
Philoliche (O.) anglulata (SIM1115) AF
Philoliche (O.) compacta (SIM1337) AF
Philoliche (Ph.) rostrata (Philros)
Philoliche (Ph.) aethiopica (Philea
Philoliche (Ph.) rubignosa (SIM
Philoliche (Ph.) elegans (SIM
Anzomyia pegasus (BDL009) AU
Anzomyia pegasus (BDL024) AU
Anzomyia pegasus (BDL074) AU
Anzomyia pegasus (BDL144) AU
NZ. gen. nov. adrel (BDL101) NZ
NZ. gen. nov. adrel (BDL102) NZ
NZ. gen. nov. milleri (BDL105) NZ
NZ. gen. nov. milleri (BDL106) NZ
NZ. gen. nov. lerda (BDL103) NZ
NZ. gen. nov. lerda (BDL104) NZ
NZ. gen. nov. ricardoae (BDL107) NZ
NZ. gen. nov. ricardoae (BDL108) NZ
Copidapha clavata (BDL077) AU
Copidapha clavata (BDL019) AU
Copidapha clavata (BDL021) AU
Copidapha subappendiculata (BDL124) AU
Copidapha regisgeorgii (BDL047) AU
Copidapha regisgeorgii (BDL091) AU
Copidapha maculiventris (BDL061) AU
Copidapha maculiventris (BDL076) AU
Copidapha maculiventris (BDL001) AU
Copidapha maculiventris (BDL018) AU
Copidapha neotricolor (BDL011) AU
Copidapha neotricolor (BDL089) AU
Copidapha neoconcolor (BDL028) AU
Copidapha bicolorata (BDL048) AU
Copidapha georgii var. (BDL050) AU
Copidapha georgii var. (BDL053) AU
Copidapha georgii (BDL051) AU
Copidapha georgii (BDL052) AU
Copidapha testaceomaculata (BDL059) AU
Copidapha testaceomaculata (BDL145) AU
Copidapha occidentalis (BDL086) AU
Copidapha occidentalis (BDL115) AU
Copidapha guttipennis (BDL140) AU
Copidapha guttipennis (BDL137) AU
Copidapha guttipennis (BDL013) AU
Copidapha guttipennis (BDL014) AU
Copidapha guttipennis (BDL023) AU
Copidapha xanthopilis (BDL060) AU
Copidapha subcontigua (BDL017) AU
Copidapha subcontigua (BDL006) AU
Copidapha subcontigua (BDL114) AU
Copidapha subcontigua (BDL148) AU
Copidapha quadrimacula (BDL081) AU
Copidapha rixei (BDL033) AU*
Copidapha neoconcolor (PEET1023) AU
Copidapha aureohirta (BDL113) AU
Copidapha lasiophthalma (BDL092) AU
Copidapha lasiophthalma (BDL027) AU
Copidapha lasiophthalma (BDL032) AU

Figure 2. Molecular phylogeny of the Scionini provided by Bayesian (PP = posterior probability; GTR + I + G; four chains; 20 M generations) and maximum likelihood (BS = bootstrap support value) analyses of combined mitochondrial (COI; COII) and nuclear loci (AATS; CAD; 28S). All branch tips have PP values of 100. Names in square parentheses refer to the old classification scheme for the newly revised genera. Tip labels refer to revised taxa. AF, Africa; AU, Australia; CA, Central America; NZ, New Zealand; SA, South America; USA, United States of America.

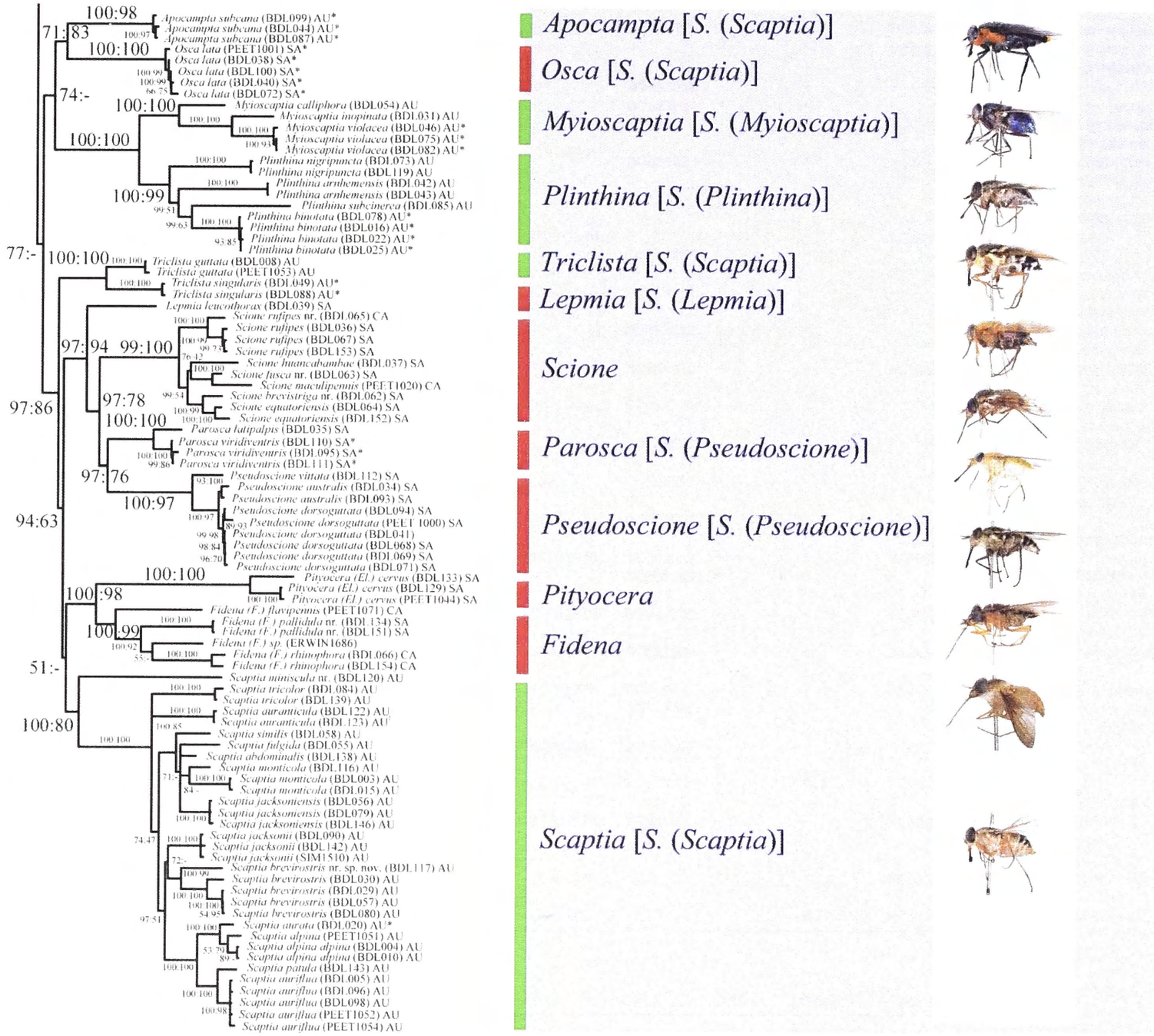

Table 1
Collection data for the austral horse fly tribe Scionini and other specimens sequence in this study. Nucleotide sequence data are deposited in Genbank and represented by accession numbers. Square parentheses refer to previously synonymised genera within *Scaptia*. Asterisk indicates type species. NP, National Park.

FAMILY SUBFAMILY Tribe	Genus	Subgenus	Species	Voucher ID	COIa	COIb	COII	AATS	CAD1	CAD3	CAD4	28Sfk	Collection data
ATHERICIDAE	*Dasyomma*	–	sp.	PEET1005	KC592664	–	–	KC592822	–	–	–	KC592526	CHILE: Chiloe, Ahoni Alto, 25–27.I.2007 B. Brown
	Atherix		*marginata*	PLIM180	KC592679	–	–	KC592835	–	–	–	KC592540	HUNGARY: Batouytereryl; Lengyendinp, 2006.07.05, M. Foldvari (NCSU)
PELECORHYNCHIDAE	*Pelecorhynchus*	–	*personatus*	Peleper	KC592677	–	–	KC592833	KC593162	–	–	KC592538	AUSTRALIA: Cooloola, Site 3, 51096 (NCSU)
TABANIDAE CHRYSOPSINAE Bouvieromyiini	*Phibalomyia*	–	*carteri*	BDL097	–	KC592911	KC593024	KC592798	–	–	–	KC592494	AUSTRALIA: QLD, Wet Tropics, Atherton uplands, rainforest, 17.61030378°S 145.76636005°E, R. Wilson (ANIC)
	Rhigioglossa	*Rhigioglossa*	*edentula*	SIM1007.1	DQ983524	–	KC593065	KC592837	DQ983564	–	–	KC592541	SOUTH AFRICA: Western Cape Province, S.I. Morita
Chrysopsini	*Chrysops*	–	*coquilletti*	CA2	DQ983512	–	KC593063	KC592819	DQ983552	–	–	KC592522	USA: California: S.I. Morita
	Silvius	–	*gigantulus*	CA6	DQ983531	–	–	–	DQ983572	–	–	–	USA: California, SI Morita
Rhinomyzini	*Tabanocella*	*Tabanocella*	*denticornis*	SIM1330.1	DQ983532	–	KC593067	KC592840	DQ983573	–	–	KC592544	USA: California, S.I. Morita
TABANINAE Diachlorini	*Agelanius* nr.	–	sp.	BDL155	–	KC592952	KC593062	–	–	–	–	–	SOUTH AFRICA: KwaZulu-Natal, S.I. Morita
	Dasybasis	*Dasybasis*	*neobasalis*	PEET1049	KC592670	–	KC593064	KC592828	KC593157	–	–	KC592532	CHILE: Region RM, El Arrayán Santuario de La Naturaleza, 33°19′15″S 70°27′13″W, El. 1073 m, 19 Jan 2011, B. Lessard, D. Amorim and D. Yeates (ANIC)
			sp.	BDL002	KC592547	KC592844	–	KC592744	–	–	–	KC592413	AUSTRALIA: NSW, Kosciusko National Park, Thredbo, 38°29′44S 148°19′15E, El. 1354 m, 23 Jan 2008, D. Carnovale, D. Yeates, C. Manchester (ANIC)
Haematopotini	*Haematopota*	–	sp.	SIM1000.1	DQ983519	–	–	–	DQ983559	–	–	–	AUSTRALIA: NSW, Perisher, Kosciuszko NP, 36°25′53″S 148°19′27″E, 12 Dec 2007 (ANIC)
Tabanini	*Hybomitra*	–	*rhombica*	CA3	DQ983520	–	–	–	DQ983560	–	–	–	SOUTH AFRICA: Western Cape Province, S.I. Morita
	Tabanus	–	*aegrotus*	CA5	DQ983533	–	–	–	DQ983574	–	–	–	USA: California, S.I. Morita
			biguttatus	SIM1321	DQ983534	–	–	–	DQ983575	–	–	–	USA: California, S.I. Morita
			sp.	BDL149	–	KC592947	KC593058	–	–	–	–	KC592521	SOUTH AFRICA: KwaZulu-Natal, S.I. Morita
PANGONIINAE Mycteromyiini	*Mycteromyia*	–	sp.	NCSU1138	KC592661	–	–	KC592821	KC593152	–	–	AF238564	AUSTRALIA: SA, Renmark, 8 Apr 2012, B. Lessard and T. Everingham (ANIC)
													CHILE (NCSU)

Pangoniini	*Esenbeckia*	*Palassomyia*	*fascipennis*	NCSU1034	KC592660	–	–	KC592820	KC593151	–	–	AF238563	CHILE (NCSU)
		Esenbeckia	*prasiniventris*	PEET1007	KC592665	–	–	KC592823	KC593153	–	–	KC592527	COSTA RICA: Caribe, Rio Francesca, 11–17.vi.2007, A. Deans (NCSU)
		Ricardoa	*delta*	PEET1070	KC592675	–	–	KC592831	KC593159	–	–	KC592536	USA: Arizona, Cochise Co., Chiricahua Mountains, 31°52′28″N 108°28′24″W, El. 1578 m, 5–12.viii.2007, J. Skevington
			sp.	PEET1025	KC592668	–	–	KC592826	–	–	–	KC592530	Mexico: Sonora, Rancho el Cajon 40 km E of Alamos, Rio Cuchujaqui, Taxodium riparian tropical deciduous forest, 27°03.00′N 108°43.91′W, El. 420 m, 1–11.x.2006 ME Irwin
	Pegasomyia	–	*abaureus*	SIM1500	DQ983523	–	–	–	DQ983563	–	–	–	USA: California, P.S. Cranston
Philolichini	*Philoliche*	*Buplex*	*basalis*	SAM2	DQ983500	–	–	KC592836	DQ983537	–	–	–	SOUTH AFRICA: Neuwoutville, S. Van Noort
			subfacia	SIM1153	DQ983501	–	–	–	DQ983538	–	–	–	SOUTH AFRICA: Hellsgate, S.I. Morita
		Dorcaloemus	*compacta*	SIM1337	DQ983502	–	–	–	DQ983539	–	–	–	ZIMBABWE: Laurenceville Rd., S.I. Morita
		Maverica	*bukamensis*	SIM1152	DQ983503	–	–	–	DQ983540	–	–	–	SOUTH AFRICA: Hellsgate, J. Esterhuizen
		Ommatiosteres	*angulata*	SIM1115	KC592680	–	–	–	DQ983545	–	–	–	SOUTH AFRICA: Pakhuis Pass, S.I. Morita
	Philoliche	*Phara*	*lateralis*	SIM1003	DQ983505	–	–	–	DQ983543	–	–	–	SOUTH AFRICA: False Bay, B.C. Anderson
			andrenoides	SIM1171	DQ983506	–	–	–	DQ983544	–	–	–	SOUTH AFRICA: Witzieshoek, S.I. Morita and SDJ
			bivirgulata	SIM1130D	DQ983508	–	–	–	DQ983546	–	–	–	SOUTH AFRICA: Shaw Farm, S.I. Morita
		Philoliche	*aethiopica*	SIM1308A	DQ983511	–	–	KC5928398	DQ983550	–	–	KC592543	SOUTH AFRICA: R102 to J-bay, S.I. Morita
			elegans	SIM1304V	DQ983514	–	–	–	DQ983554	–	–	–	SOUTH AFRICA: Glen Craig Farm, S.I. Morita
			rostrata	Philros	KC592678	–	–	KC592834	KC593163	–	–	KC592539	SOUTH AFRICA: S.I. Morita
			rubignosa	SIM1149	DQ983526	–	–	–	DQ983566	–	–	–	SOUTH AFRICA: Hellsgate, S.I. Morita
		Returneria	*alternans*	SIM1409	–	–	–	KC592841	DQ983548	–	–	KC592545	SOUTH AFRICA: Westcoast Fossil Park, M. Buffington
Scionini	*Anzomyia*	–	*pegasus*	BDL009	KC592550	–	KC592959	KC592749	KC593072	–	KC593198	KC592419	AUSTRALIA: NSW, Kosciuszko NP, 1.7 km ENE Thredbo, 36°30′07″S 148°19′02″E, El. 1380 m, 2–11 Jan 2004, C.L. Lambkin and N.T. Starick, (ANIC)
				BDL024	KC592562	KC592858	–	–	–	–	KC593210	KC592432	AUSTRALIA: NSW, Kosciuszko NP, 0.8 km NE Thredbo, 36°29′49″S 148°18′51″E, El. 1480 m, C.L. Lambkin and N.T. Starick (ANIC)

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Table 1 (*continued*)

FAMILY SUBFAMILY Tribe	Genus	Subgenus	Species	Voucher ID	COIa	COIb	COII	AATS	CAD1	CAD3	CAD4	28Sfk	Collection data
				BDL074	KC592606	–	KC593005	–	KC593112	KC592709	KC593236	–	AUSTRALIA: NSW, Kosciuszko NP, 36°30′07″S 148°19′02″E, 2–11.i.2004, C.L. Lambkin and N.T. Starick (ANIC)
				BDL144	–	KC592944	–	–	–	–	KC593272	–	AUSTRALIA: NSW, Kosciuszko NP, 1.8 km NE Thredbo, 36°29′49″S 148°18′51″E, El. 1480 m, 2–11 Jan 2004, C.L. Lambkin and N.T. Starick (ANIC)
	Goniops	–	*chrysocoma*	SIM1151	KC592681	–	KC593066	KC592838	KC593164	–	–	KC592542	USA: Maryland, Little Orleans, June 2007, M. Bertone (NCSU)
				BDL130	KC592648	KC592936	KC593049	–	–	–	–	KC592513	USA: West Virginia, Hardy Co., 14–31 Jul 2007, D. Smith (NCSU)
	Pityocera	*Elaphella*	*cervus*	PEET1044	KC592669	–	–	KC592827	KC593156	–	–	KC592531	FRENCH GUIANA: Regina; Point Rd., Kaw Mountains 4°33′19″N 52°09′59″W, El. 300 m, 8–9 Mar 2006, K. Sarv
				BDL129	KC592647	KC592935	KC593048	–	KC593149	–	KC593267	KC592512	FRENCH GUIANA: Regina, Point Rd., Kaw Kaw Mountains, 4°33′19″N 52°09′59″W, El. 300 m, 3–27 Mar 2007, K. Sarv
				BDL133	KC592649	KC592937	KC593050	KC592811	KC593150	–	KC593268	–	PERU: Rio Tambopata, Explorers Inn Rio Tower, 12°50.208′S 69°17.603′W, 6–13.xii.2003, Svenson, Miller, Osborne and Ogden (BYU)
	Scione	–	*brevistriga* nr.	BDL062	KC592597	KC592883	KC592995	KC592774	KC593103	KC592703	KC593186	KC592466	ECUADOR: Pichincha, Los Cedros, 11 Aug 2007, R. Cardenas
			equatoriensis	BDL064	KC592599	KC592885	KC592997	KC592775	KC593105	–	KC593188	KC592468	ECUADOR: Pichincha, Yanacocha, 00°06.962′S 78°35.088′W, El. 3562 m, 3 Aug 2009, D. Ramirez (NCSU)
				BDL152	KC592657	KC592949	–	KC592817	–	KC592741	KC593165	–	ECUADOR: Pichincha, Los Cedros, 8.viii.2007, R. Cardenas
			fusca nr.	BDL063	KC592598	KC592884	KC592996	–	KC593104	KC592704	KC593187	KC592467	ECUADOR: Pichincha, Los Cedros, El. 1350 m, R. Cardenas
			huancabambae	BDL037	KC592573	KC592862	KC592972	–	KC593086	KC592694	KC593172	KC592443	ARGENTINA: Jujuy, Calilegua NP, 23°42′00″S 64°52′00″W, El. 1081 m, 12.xi.2008, J. Skevington
			maculipennis	PEET1020	KC592666	–	–	KC592824	KC593154	–	–	KC592528	COSTA RICA: Cacao La Cim, 19 Apr 1999, A. Deans (NCSU)

			rufipes	BDL036	KC592572	KC592861	KC592971	KC592759	KC593085	–	KC593171	KC592442	PERU: Cock of the Rock Lodge, 13°03′21″S. 71°32′46″W, El. 1380 m, 18–20.x.2006, J. Skevington
				BDL067	KC592602	KC592888	KC593000	KC592778	KC593107	–	KC593190	KC592471	PERU: Cock of the Rock Lodge, 13°03′21″S 71°32′46″W, El. 1380 m, 18–20 Oct 2006, J. Skevington
				BDL153	–	KC592950	KC593060	–	–	–	KC593166	–	PERU: Cock of the Rock Lodge, 13°03′21″S 71°32′46″W, El. 1380 m, 18–20 Oct 2006, J. Skevington
			rufipes nr.	BDL065	KC592600	KC592886	KC592998	KC592776	KC593106	–	KC593189	KC592469	PANAMA: Chirqui Prov., Fortuna Reserve, 8°44.840′N 82°14.562′W, El. 1151 m, 30 Aug 2008, A. Gillogly and A. Smith
Fidena	*Fidena*		*flavipennis*	PEET1071	KC592676	–	–	KC592832	KC593161	–	–	KC592537	COSTA RICA: Limon Prov., Talamanca de Punta Uva, 9°37′24″N 82°40′51″W, 28 Jul 2007, L. Forehand
			pallidula nr.	BDL134	KC592650	KC592938	KC593051	KC592812	–	–	KC593269	KC592514	PERU: Rio Tambopata, Explorers Inn Rio Tower, 12°50.208′S 69°17.603′W, 6–13.xii.2003, Svenson, Miller, Osborne and Ogden (BYU)
				BDL151	KC592656	KC592948	KC593059	KC592816	–	KC592740	KC593275	–	PERU: Rio Tambopata, 12°50.208″S 69°17.603″W, 6–13 Dec 2003, Svenson, Miller, Osborne and Ogden (BYU)
			rhinophora	BDL066	KC592601	KC592887	KC592999	KC592777	KC593160	KC592705	KC593230	KC592470	ECUADOR: Pichincha, nr Mindo, July 2009, R. Cardenas, K. Bayless and D. Ramirez (NCSU)
				BDL154	KC592658	KC592951	KC593061	KC592818	–	KC592742	KC593276	–	PANAMA: Chiriqui Prov., Reserva Fortuna, 8°45.468′N 82°15.671′W, El. 1235–1300 m, 1.x.2008, Gillogly
			sp.	ERWIN1686	KC592659	–	–	–	–	–	–	KC592523	ECUADOR: Yasuni Park, T. Erwin
Scaptia	*Scaptia*		*abdominalis*	BDL138	–	KC592940	KC593053	KC592813	–	–	–	–	AUSTRALIA: Vic, Mt Baw Baw BP, Big Tree Creek, 37°49′53″S 146°11′37″E, El. 216 m, 8.xii.2011 (ANIC)
			alpina alpina	BDL004	–	KC592845	KC592955	KC592745	KC593069	KC592684	–	KC592415	AUSTRALIA: NSW, Guthega, Kosciusko NP (ANIC)
				BDL010	–	KC592848	KC592960	–	–	–	–	KC592420	AUSTRALIA: NSW, Kosciuszko NP, 1.7 km ENE Thredbo, 36°30′07″S

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Table 1 (*continued*)

FAMILY SUBFAMILY Tribe	Genus	Subgenus	Species	Voucher ID	COIa	COIb	COII	AATS	CAD1	CAD3	CAD4	28Sfk	Collection data
			alpina	PEET1051	KC592671	–	–	–	–	–	–	KC592533	148°19′02″E, 2–11 Jan 2004, C. Lambkin and N. Starick (ANIC) AUSTRALIA: NSW, Kosciuszko National Park, Thredbo, 36°29′44″S E148°18′15″E, El. 1354 m, 23 Jan 2008, D. Carnovale, D. Yeates and C. Manchester
			*aurata**	BDL020	KC592558	KC592854	–	KC592753	–	–	–	–	AUSTRALIA: NSW, Morton NP Tianjara Falls, 35°06′38″S 150°19′54″E, 29 Nov 2003 (ANIC)
			auranticula	BDL122	–	KC592932	KC593046	KC592809	–	–	–	–	AUSTRALIA: WA, Porongerups NP, 34°40.384′S 117°53.511′E, El. 351 m, 3–15 Nov 2003, C. Lambkin and J. Recsei (ANIC)
				BDL123	–	KC592933	KC593047	KC592810	KC593148	–	KC593185	–	AUSTRALIA: WA, Porongerups NP, 34°40.384′S 117°53.511′E, El. 351 m, 3–15 Nov 2003, C. Lambkin and J. Recsei (ANIC)
			auriflua	BDL005	KC592548	KC592846	KC592956	KC592746	KC593070	KC592685	KC593167	KC592416	AUSTRALIA: Canberra, ACT, 18 Dec 2007, D. Yeates (ANIC)
				BDL096	KC592626	KC592910	KC593023	KC592797	–	KC592725	–	KC592493	AUSTRALIA: Tas, Central Plateau Plantation area, S of Deloraine, 41.7104°S 146.72877°E, 30.i.2010, B. Lessard, N. Gunter and K. Meiklejohn (ANIC)
				BDL098	KC592627	KC592912	KC593025	KC592799	KC593129	KC592726	KC593178	KC592495	AUSTRALIA: ACT, Black Mountain, 18 Nov 2012, D. Yeates (ANIC)
				PEET1052	KC592672	–	–	–	–	–	–	–	AUSTRALIA: ACT, Canberra, 18.12.2007 D. Yeates (ANIC)
				PEET1054	KC592674	–	–	KC592830	–	–	–	KC592535	AUSTRALIA: NSW, Talaganda National park, S35°24′53 E149°32′07, El. 1140 m, 15 Jan 2008, D. Yeates, D. Carnovale and C. Manchester
			brevirostris	BDL029	KC592565	–	–	KC592758	KC593082	KC592693	KC593168	KC592435	AUSTRALIA: QLD, Daintree NP, Cape Tribulation, 16°14.311′S 145°25.945′E, El. 40 m, 18–19 Dec 2005, A. Deans and M. Buffington (NCSU)

	BDL030	KC592566	–	–	–	–	–	KC593169	KC592436	AUSTRALIA: QLD, Ravenshoe State Forest, 17°44′S 145°32′E, Nov 1999, M. Mathieson (NCSU)
	BDL057	KC592592	KC592878	KC592990	KC592772	KC593099	–	KC593176	KC592461	AUSTRALIA: NSW, 800 m S Wards Gulley Creek on Armidale Rd., 29°59′40″S 152°42′35″E, El. 298 m, 26.xi.2009, B. Lessard, L. Nelson, A. Thornhill and D. Yeates (ANIC)
	BDL080	KC592612	KC592898	KC593011	KC592788	KC593116	KC592715	KC593192	KC592481	AUSTRALIA: NSW, Washpool, 29°28′16″S 152°19′14″E, El. 901 m, 28.xi.2009, B. Lessard, L. Nelson, A. Thornhill and D. Yeates (ANIC)
brevirostris nr.	BDL117	KC592644	KC592929	KC593043	KC592807	KC593145	KC592734	KC593180	–	AUSTRALIA: QLD, Cape Tribulation NP, Dubuji-Myall Beach, 16°5.61S 145°27.736′E, 12.iii.2011, S. Cameron (ANIC)
fulgida	BDL055	KC592590	KC592876	KC592988	KC592771	KC593097	–	KC593174	KC592459	AUSTRALIA: QLD, Lamington NP, 28.192°S 153.124°E, 2–16 Dec 2008, G. Monteith (QM)
jacksoniensis	BDL056	KC592591	KC592877	KC592989	–	KC593098	KC592700	KC593175	KC592460	AUSTRALIA: NSW, Morton NP, 35°04′33″S 150°09′08″E, 17 Nov 2009, B. Lessard, C. Manchester and D. Yeates (ANIC)
	BDL079	KC592611	KC592897	KC593010	KC592787	–	KC592714	KC593191	KC592480	AUSTRALIA: NSW, Morton NP, 35°01′56″S 150°08′07″E, 17–23.xi.2009, B. Lessard, C. Manchester and D. Yeates (ANIC)
	BDL146	KC592655	–	KC593057	–	–	KC592738	KC593184	KC592520	AUSTRALIA: Vic, Bull Creek Divide, Mitchell River NP, 37°41′16″S 147°20′46″E, El. 54 m, 9 Dec 2011 (ANIC)
jacksonii	BDL090	KC592621	KC592906	KC593019	KC592794	KC593124	KC592722	KC593194	KC592488	AUSTRALIA: Tas, N of Tarraleah, 42.26671S 146.4745E, 28.i.2010, B. Lessard, K. Meiklejohn and N. Gunter (ANIC)
	BDL142	–	KC592942	–	KC592815	–	–	–	KC592518	AUSTRALIA: Tas, Keoghs Creek on Arve Road, Southern Forests, 43.15122S 146.79369E, 14.i.2012, J. Mynott and M. Shackleton (ANIC)
	SIM1510	KC592682	–	–	KC592842	–	–	–	–	AUSTRALIA: Tas (NCSU)
monticola	BDL003	–	–	KC592954	–	–	–	–	KC592414	AUSTRALIA: NSW, East Boyd State Forest, 37°12′05″S 149°46′30″E, 6 Dec 2004 (ANIC)
	BDL015	KC592553	–	KC592963	–	–	–	KC593202	KC592424	AUSTRALIA: NSW,

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Table 1 (*continued*)

FAMILY SUBFAMILY Tribe	Genus	Subgenus	Species	Voucher ID	COIa	COIb	COII	AATS	CAD1	CAD3	CAD4	28Sfk	Collection data
				BDL116	–	KC592928	KC593042	–	KC593144	KC592733	KC593179	KC592510	Yambulla State NP, 37°11′52″S 149°37′02″W, El. 299 m, 14 Feb – 9 Mar 2005, C. Lambkin and N. Starick (ANIC) AUSTRALIA: QLD, Colosla, 7.x.2002, B. Wiegmann (NCSU)
			miniscula nr.	BDL120	–	KC592931	KC593045	–	KC593147	KC592736	KC593181	KC592511	AUSTRALIA: NSW, Washpool, 29°28′16″S 152°19′14″E, El. 901 m, 29.xi.2009, B. Lessard, L. Nelson, A. Thornhill and D. Yeates (ANIC)
			patula	BDL143	KC592653	KC592943	KC593056	–	–	–	KC593183	–	AUSTRALIA: NSW, Warrumbungle NP, Buckleys Creek, 31°16.083′S 149°00.04′E, El. 298 m, 19.iii-8.iv.2008, S.L. Winterton, J.S. Bartlett and D.J. Tree
			similis	BDL058	KC592593	KC592879	KC592991	–	–	–	KC593177	KC592462	AUSTRALIA: QLD, Cainbable Quarry, 28.145°S 153.113°E, 28 Oct – 9 Nov 2008, G Monteith (QM)
			tricolor	BDL084	KC592615	KC592901	–	–	–	–	KC593193	–	AUSTRALIA: WA, Blue Lake, Mt Lindesay NP, 34°46′10″S 117°16′35″E, El. 195 m, 5 Oct 2010, B. Lessard and N. Gunter (ANIC)
				BDL139	KC592652	–	KC593054	KC592814	–	–	KC593182	KC592516	AUSTRALIA: WA, Scott NP, 34°17′01″S 115°05′51″E, El. 190 m, 1.x.2010, B. Lessard and N. Gunter (ANIC)
	[*Apocampta*]		*subcana**	BDL044	KC592580	KC592868	KC592979	–	–	–	KC593218	KC592449	AUSTRALIA: QLD, Bribie Island, 27.053′S 153.180′E, 17 Oct 2007, S. Winterton (NCSU)
				BDL087	KC592618	KC592903	KC593016	KC592792	KC593121	KC592719	KC593245	KC592485	AUSTRALIA: QLD, Brisbane Forest Pk, 27.427°S 152.841°E, 13 Dec 2007–17 Jan 2008, S. Winterton and J. Bartlett (NCSU)
				BDL099	KC592628	KC592913	KC593026	KC592800	–	KC592727	KC593252	KC592496	AUSTRALIA: QLD, Bribie Island, Heathland, 27.053°S 153.180°E, 17.x.2007, S.L. Winterton (NCSU)

[*Triclista*]		*guttata*	BDL008	KC592549	–	KC592958	KC592748	KC593071	–	KC593197	KC592418	AUSTRALIA: NSW, Nelligen, 35°38′52″S 150°08′29″E, 11 Feb 2008, D. Yeates (ANIC)
			PEET1053	KC592673	–	–	KC592829	KC593158	–	–	KC592534	AUSTRALIA: NSW, Nelligen, 35°38′52″S 150°08′29″E, 11 Feb 2008, D. Yeates (ANIC)
		*singularis**	BDL049	KC592584	KC592871	–	KC592766	–	–	KC593221	KC592453	AUSTRALIA: WA, nr. Roleystone, 32°07′20″S 116°01′52″E, El. 46 m, 9 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
			BDL088	KC592619	KC592904	KC593017	KC592793	KC593122	KC592720	KC593246	KC592486	AUSTRALIA: WA, Armadale, 32°07′13″S 116°01′21″E, El. 57 m, 15 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
[*Osca*]		*lata**	BDL038	KC592574	KC592863	KC592973	KC592760	KC593087	–	KC593214	KC592444	CHILE: Los Lagos, Parque Nacional Alerce Andino, Chaicra, i.2007, B. Brown
			BDL040	KC592576	KC592865	KC592975	KC592761	KC593089	–	KC593215	KC592446	CHILE: Los Lagos, Parque Nacional Alerce Andino, Chaicra, i.2007, B. Brown
			BDL072	–	KC592891	KC593003	KC592782	KC593110	KC592707	KC593234	KC592475	CHILE: Los Lagos Prov., Parque Nacional Alerce Andino, Chaicra, i.2007, B. Brown
			BDL100	KC592629	KC592914	KC593027	KC592801	KC593130	KC592728	KC593253	–	CHILE: Los Lagos Prov., Petrohue River, Ensenada, 41°09′14″S 72°26′00″W, El. 173 m, 9.ii.2011, B. Lessard, D. Amorim and D. Yeates (ANIC)
			PEET1001	KC592663	–	–	–	–	–	–	KC592525	ARGENTINA: Neuquen Prov., Parque Nacional Lanin, 1.5 km N Puerto Canoa, 39°44.02′S 71°30.86′W, El. 1010 m, 25.xii.2005–2.i.2006, M. Irwin
[*Lepmia*]		*leucothorax*	BDL039	KC592575	KC592864	KC592974	–	KC593088	KC592695	–	KC592445	CHILE: Región Metropolitana, Yeso Road, Valle Del Rio Volcan, 33°47′33″S 70°12′07″W, El. 1325 m, 18 Nov 2008, J. Skevington
[*Myioscaptia*]	*Myioscaptia*	*calliphora*	BDL054	KC592589	KC592875	KC592987	KC592770	KC593096	KC592699	KC593226	KC592458	AUSTRALIA: NSW, Morton NP, 35°02′35″S 150°08′31″E, 17.xi.2009, B. Lessard, C. Manchester and D. Yeates (ANIC)
		inopinata	BDL031	KC592567	–	KC592969	–	KC593083	–	KC593170	KC592437	AUSTRALIA: QLD, State Forest 607, 16°59′S 145°36′E, Nov 1999, M. Mathieson (ANIC)
		*violacea**	BDL046	KC592581	KC592869	KC592980	KC592765	–	–	KC593219	KC592450	AUSTRALIA: NSW, Thunderbolts Way nr. Giro, 31°44′37″S 151°52′49″E, El. 164 m, 1.xii.2009, B. Lessard, L. Nelson, A. Thornhill and D. Yeates

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Table 1 (*continued*)

FAMILY SUBFAMILY Tribe	Genus	Subgenus	Species	Voucher ID	COIa	COIb	COII	AATS	CAD1	CAD3	CAD4	28Sfk	Collection data
				BDL075	KC592607	KC592893	KC593006	–	–	KC592710	KC593237	–	(ANIC) AUSTRALIA: NSW, Washpool, 29°28′16″S 152°19′14″E, El. 901 m, 28.xi.2009, B. Lessard, L. Nelson, A. Thornhill and D. Yeates (ANIC)
				BDL082	KC592614	KC592900	KC593013	KC592790	KC593118	KC592717	KC593242	KC592483	AUSTRALIA: NSW, Washpool, 29°28′16″S 152°19′14″E, El. 901 m, 28.xi.2009, B. Lessard, L. Nelson, A. Thornhill and D. Yeates (ANIC)
	[*Plinthina*]	*Plinthina*	*arnhemensis*	BDL042	KC592578	KC592867	KC592977	KC592763	KC593090	KC592696	KC593217	–	AUSTRALIA: NT, NE Arnhemland, 12°23′02″S, 136°37′42″E, 16–27 Aug 2007, D. Yeates, C. Manchester and S. Winterton (ANIC)
				BDL043	KC592579	–	KC592978	KC592764	–	–	–	KC592448	AUSTRALIA: NT, NE Arnhemland, 12°23′15″S, 136°36′01″E, 16–27 Aug 2007, D. Yeates, C. Manchester and S. Winteron (ANIC)
			binotata	BDL016	KC592554	KC592851	KC592964	–	KC593075	KC592688	KC593205	KC592425	AUSTRALIA: WA, Heinsmen Rock, 33°07.020′S 123°27.077′E, El. 145 m, 30 Oct – 18 Nov 2003, C. Lambkin and J. Rescsei (ANIC)
				BDL022	KC592560	KC592856	KC592967	KC592755	KC593079	KC592691	KC593208	KC592430	AUSTRALIA: WA, Heinsmen Rock, 33°07.020′S 123°27.077′E, El. 145 m, 30 Oct–18 Nov 2003, C. Lambkin and J. Rescsei (ANIC)
				BDL025	KC592563	–	KC592968	KC592757	KC593081	–	–	KC592433	AUSTRALIA: WA, Pine Hill, Cape Arid NP, 33°18.065′S 123°22.274′E, El. 130 m, 31.x-18.xi.2003, C. Lambkin and J. Recsei (ANIC)
				BDL078	KC592610	KC592896	KC593009	KC592786	KC593115	KC592713	KC593240	KC592479	AUSTRALIA: WA, Pine Hill, 33°18.065′S 123°22.274′E, El. 130 m, 31.x-18.xi.2003, C. Lambkin and J. Recsei (ANIC)
			nigripuncta	BDL073	KC592605	KC592892	KC593004	KC592783	KC593111	KC592708	KC593235	KC592476	AUSTRALIA: QLD, Mt Glorious, 27°20′S 152°46′E, El. 660 m, 12 Dec 1998–28 Jan 1999, N. Power (QM)

				BDL119	KC592645	KC592930	KC593044	KC592808	KC593146	KC592735	KC593266	–	AUSTRALIA: QLD, Lamington NP, rainforest, 28.227°S 153.131°E, El. 920 m, 14–24.i.2007, C. Lambkin and N. Starick (QM)
			subcinerea	BDL085	KC592616	–	KC593014	–	KC593119	–	KC593243	–	AUSTRALIA: WA, Colletts Road, nr Fitzgerald River NP, 34°08′55″S 119°14′27″E, El. 30 m, 7 Oct 2010, B. Lessard and N. Gunter (ANIC)
[*Copidapha*]	*Pseudoscione*		*aureohirta*	BDL113	KC592641	KC592925	KC593039	KC592804	KC593141	KC592730	KC593263	KC592507	AUSTRALIA: QLD, Byfield State Forest, 22°57′27″S 150°40′50″E, El. 51 m, 11.i.2010 (ANIC)
			bicolorata	BDL048	KC592583	KC592870	KC592982	–	KC593092	KC592697	KC593220	KC592452	AUSTRALIA: WA, nr. Roleystone, 32°07′20″S 116°01′52″E, El. 46 m, 9 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
			clavata	BDL019	KC592557	KC592853	KC592966	KC592752	KC593077	KC592690	KC593203	KC592428	AUSTRALIA: NSW, East Boyd State Forest, Goanna Rd., 56 km SE Bombala, 37°12′05″S 149°46′30″E, El. 219 m, 14 Feb–9 Mar 2005, C. Lambkin and N. Starick (ANIC)
				BDL021	KC592559	KC592855	–	KC592754	KC593078	–	KC593204	KC592429	AUSTRALIA: NSW, Bluebell Swamp, Tinderry Nat. Res., 11.5 km ENE Michelago, 35°41′02″S 148°17′16″E, El. 1243 m, 29 Jan–26 Feb 2005, C. Lambkin and N. Starick (ANIC)
				BDL077	KC592609	KC592895	KC593008	KC592785	KC593114	KC592712	KC593239	KC592478	AUSTRALIA: NSW, Tinderry Nat. Res., 13.3 km ENE Michelago, 35°40′51″S 149°18′26″E, El. 1065 m, C Lambkin and N Starick (ANIC)
			georgii	BDL051	KC592586	–	KC592984	KC592767	KC593093	–	KC593223	KC592455	AUSTRALIA: WA, Leeuwin-Naturaliste NP, 33°51′11″S 115°01′38″E, El. 85 m, 11 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
				BDL052	KC592587	KC592873	KC592985	KC592768	KC593094	–	KC593224	KC592456	AUSTRALIA: WA, Giant Tingle Tree, 34°58′57″S 116°47′25″E, El. 175 m, 13 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
			georgii var.	BDL050	KC592585	KC592872	KC592983	–	–	KC592698	KC593222	KC592454	AUSTRALIA: WA, Donnelly River, 34°19′49″S 115°46′38″E, El. 27 m, 12 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
				BDL053	KC592588	KC592874	KC592986	KC592769	KC593095	–	KC593225	KC592457	AUSTRALIA: WA, Walpole,

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Table 1 (*continued*)

FAMILY SUBFAMILY Tribe	Genus	Subgenus	Species	Voucher ID	COIa	COIb	COII	AATS	CAD1	CAD3	CAD4	28Sfk	Collection data
													34°58′26″S 116°42′47″E, El. 10 m, 13 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
			guttipennis	BDL013	KC592551	KC592849	–	KC592750	KC593073	KC592687	KC593200	KC592422	AUSTRALIA: WA, Heinsmen Rock, 33°07.020′S 123°27.077′E, El. 145 m, 30 Oct–18 Nov 2003, C. Lambkin and J. Recsei (ANIC)
				BDL014	KC592552	KC592850	KC592962	–	KC593074	–	KC593201	KC592423	AUSTRALIA: WA, Heinsmen Rock, 33°07.020′S 123°27.077′E, El. 145 m, 30 Oct–18 Nov 2003, C. Lambkin and J. Recsei (ANIC)
				BDL023	KC592561	KC592857	–	KC592756	KC593080	KC592692	KC593209	KC592431	AUSTRALIA: WA, Pine Hill, Cape Arid NP, 33°18.065′S 123°22.274′E, El. 130 m, 31 Oct – 18 Nov 2003, C Lambkin and J Rescei (ANIC)
				BDL137	KC592651	KC592939	KC593052	–	–	–	KC593270	KC592515	AUSTRALIA: WA, Eucla Caravan Park, 31°40′39.8″S 128°52′54.7″E, 6.ix.2011, A. Thornhill (ANIC)
				BDL140	–	KC592941	KC593055	–	–	–	KC593271	KC592517	AUSTRALIA: SA, Coffin Bay, 18.x.2009, N Starick and C Lambkin (QM)
			lasiopthalma	BDL027	KC592564	–	–	–	–	–	–	–	AUSTRALIA: QLD, Ravenshoe State Forest, 17°44′S 145°32′E, Nov 1999, M. Mathieson
				BDL032	KC592568	–	–	–	–	–	KC593211	KC592438	AUSTRALIA: QLD, Ebony Road, Ravenshoe State Forest, 17°44′S 145°33′E, Nov 1999, M. Mathieson
				BDL092	–	–	–	–	–	–	KC593248	–	AUSTRALIA: QLD, Ravenshoe State Forest, 17°44′S 145°32′E, Nov 1999, M. Mathieson
			maculiventris	BDL001	KC592546	KC592843	KC592953	KC592743	KC593068	KC592683	KC593195	KC592412	AUSTRALIA: NSW, Kosciusko National Park, Perisher 36°21′46″S 148°28′51″E, 11 Dec 2007 (ANIC)
				BDL018	KC592556	KC592852	KC592965	KC592751	KC593076	KC592689	KC593207	KC592427	AUSTRALIA: ACT, Mt Ginini, 35°31′36″S 148°46′45″E, El. 1675 m, 5 Dec 2007, D. Carnovale, C. Manchester, A. Cardilini and V. Hatton (ANIC)

		BDL061	KC592596	KC592882	KC592994	KC592773	KC593102	KC592702	KC593229	KC592465	AUSTRALIA: NSW, Morton NP, 35°04′33″S 150°09′08″E, 17.xi.2009, B. Lessard, C. Manchester and D. Yeates (ANIC)
		BDL076	KC592608	KC592894	KC593007	KC592784	KC593113	KC592711	KC593238	KC592477	AUSTRALIA: NSW, Morton NP, 35°01′56″S 150°08′07″E, 23.xi-1.xii.2009, B. Lessard, C. Manchester and D. Yeates (ANIC)
	neoconcolor	BDL028	–	–	–	–	–	–	–	KC592434	AUSTRALIA: QLD, Ravenshoe State Forest, 17°44′S 145°32′E, Nov 1999, M. Mathieson
		PEET1023	KC592667	–	–	KC592825	KC593155	–	–	KC592529	AUSTRALIA: QLD, Daintree NP, Mossman Gorge Park, 19 Dec 2005 (NCSU)
	neotricolor	BDL011	–	–	KC592961	–	–	KC592686	KC593199	KC592421	AUSTRALIA: WA, Cockleshell Gulley Lesuer NP, 30°08′47″S 115°06′27″E, El. 59 m, 20 Sept – 9 Nov 2003, C. Lambkin and J. Recsei (ANIC)
		BDL089	KC592620	KC592905	KC593018	–	KC593123	KC592721	KC593247	KC592487	AUSTRALIA: WA, Hillview lookout, Augusta, 34°17′54″S 115°16′12″E, El. 20 m, 1 Oct 2010, B. Lessard and N. Gunter (ANIC)
	occidentalis	BDL086	KC592617	KC592902	KC593015	KC592791	KC593120	KC592718	KC593244	KC592484	AUSTRALIA: WA, Colletts Rd nr. Fitzgerald NP, 34°08′55″S 119°14′27″E, El. 30 m, 7 Oct 2010, B. Lessard and N. Gunter (ANIC)
		BDL115	KC592643	KC592927	KC593041	KC592806	KC593143	KC592732	KC593265	KC592509	AUSTRALIA: WA, Stirling Ranges, Gnowellen Road, 34°20′12″S 118°23′49″E, El. 164 m, B. Lessard and N. Gunter (ANIC)
	quadrimacula	BDL081	KC592613	KC592899	KC593012	KC592789	KC593117	KC592716	KC593241	KC592482	AUSTRALIA: NSW, Thunderbolts Way, nr. Giro, 31°44′37″S 151°52′49″E, 20.XI.2009, B. Lessard, L. Nelson, A. Thornhill and D. Yeates (ANIC)
	regisgeorgii	BDL047	KC592582	–	KC592981	–	KC593091	–	KC593173	KC592451	AUSTRALIA: WA, Calgardup Caves Carpark, 34°03′01″S 115°01′30″E, El. 82 m, 11 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
		BDL091	KC592622	–	–	–	KC593125	–	–	KC592489	AUSTRALIA: WA, Leeuwin-Naturaliste NP, 33°51′11″S 115°01′38″E, El. 85 m, 11 Dec 2009, B. Lessard and K. Meiklejohn (ANIC)
	*roei**	BDL033	KC592569	–	–	–	–	–	KC593212	KC592439	AUSTRALIA: QLD,

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Table 1 (*continued*)

FAMILY SUBFAMILY Tribe	Genus	Subgenus	Species	Voucher ID	COIa	COIb	COII	AATS	CAD1	CAD3	CAD4	28Sfk	Collection data
			subappendiculata	BDL124	KC592646	KC592934	–	–	–	–	–	–	Ravenshoe State Forest, 17°44′S 145°32′E, Nov 1999, M. Mathieson
			subcontigua	BDL006	–	KC592847	KC592957	KC592747	–	–	KC593196	KC592417	AUSTRALIA: QLD, Belah St, Mt Crosby, 27.53°S 152.84°E, Mar 2011, M. Gunter (ANIC)
				BDL017	KC592555	–	–	–	–	–	KC593206	KC592426	AUSTRALIA: NSW, East Boyd State Forest, Goanna Rd., 56 km SE Bombala, 37°12′05″S 149°46′30″E, El. 219 m, 6 Dec 2004–12 Jan 2005 (ANIC)
				BDL114	KC592642	KC592926	KC593040	KC592805	KC593142	KC592731	KC593264	KC592508	AUSTRALIA: NSW, East Boyd State Forest, Goanna Rd., 56 km SE Bombala, 37°12′05″S 149°46′30″E, El. 219 m, 6 Dec 2004–12 Jan 2005 (ANIC)
				BDL148	–	KC592946	–	–	–	KC592739	KC593274	–	AUSTRALIA: NSW, Berry Beach, nr. Seven Mile Beach NP, 26.i.2010, B. Lessard (ANIC)
			testaceomaculata	BDL059	KC592594	KC592880	KC592992	–	KC593100	KC592701	KC593227	KC592463	AUSTRALIA: NSW, Durrus North Caravan Park, 13 Jan 2012, G. Teakle (ANIC)
				BDL145	KC592654	KC592945	–	–	–	KC592737	KC593273	KC592519	AUSTRALIA: NSW, Morton NP, 35°02′35″S 150°08′31″E, 17.xi.2009, B. Lessard, C. Manchester and D. Yeates (ANIC)
			xanthopilis	BDL060	KC592595	KC592881	KC592993	–	KC593101	–	KC593228	KC592464	AUSTRALIA: Vic, Mitchell River NP, Bull Creek Divide, 37°41′16″S 147°20′46″E, El. 54 m, 09 Dec 2011 (ANIC)
[*Pseudoscione*]	*Pseudoscione*		*australis*	BDL034	KC592570	KC592859	–	–	–	–	–	KC592440	AUSTRALIA: QLD, Lamington NP, 28.210°S 153.127°E, 9 Nov–2 Dec 2008, G. Monteith (QM)
				BDL093	KC592623	KC592907	KC593020	KC592795	KC593126	KC592723	KC593249	KC592490	ARGENTINA: Chubut Prov., 2 km SE Alerces NP, 42°59.36′S 71°33.99′W, El. 590 m, 23–31 Dec 2005, ME Irwin
													CHILE: Region X, Volcan Osorno, Parque Nacional Vicente Perez Rosales, 41°08′29″S 72°32′06″W, El. 895 m, 9.ii.2011, B. Lessard, D. Amorim and D. Yeates (ANIC)

		dorsoguttata	BDL041	KC592577	KC592866	KC592976	KC592762	–	–	KC593216	KC592447	ARGENTINA: Chubut Prov., 2 km SE Alerces NP, 42°59.36′S 71°33.99′W, 23–31 Dec 2005, M.E. Irwin
			BDL068	KC592603	KC592889	KC593001	KC592779	KC593108	KC592706	KC593231	KC592472	ARGENTINA: Rio Negro Prov., Nahuel Haupi, Rio Negro NP, 41°22.49″S 71°44.16″W, 10 Feb 2010 (ANIC)
			BDL069	KC592604	KC592890	KC593002	KC592780	KC593109	–	KC593232	KC592473	ARGENTINA: Chubut Prov., Cholola, 42°27.02′S 71°27.00′W, El. 560 m, 23–31 Dec 2005, M. Irwin
			BDL071	–	–	–	KC592781	–	–	KC593233	KC592474	ARGENTINA: Chubut Prov., 2 km SE entrance to Alerces NP, 42°59.36″S 71°33.99″W, El. 590 m, M. Irwin
			BDL094	KC592624	KC592908	KC593021	KC592796	KC593127	KC592724	KC593250	KC592491	CHILE: Region IX, Parque Nacional Volcan Villarreca, 39°23′23″S 71°57′44″W, El. 1379 m, 6.ii.2011, B. Lessard, D. Amorim and D. Yeates (ANIC)
			PEET1000	KC592662	–	–	–	–	–	–	KC592524	ARGENTINA: Neuquen Prov., Parque Nacional Lanin, 1.5 km N Puerto Canoa, 39°44.02′S 71°30.86′W, El. 1010 m, 25.xii.2005–2.i.2006, M. Irwin
		vittata	BDL112	KC592640	KC592924	KC593038	KC592803	–	KC592729	KC593262	KC592506	CHILE: Los Vilos, 31°59′32″S 71°30′35″W, El. 31 m, 23.i.2011, B. Lessard, D. Amorim and D. Yeates (ANIC)
	[*Parosca*]	*latipalpis*	BDL035	KC592571	KC592860	KC592970	–	KC593084	–	KC593213	KC592441	CHILE: Los Lagos, Parque Nacional Alerce Andino, Chaicra, i.2007, B. Brown
		*viridiventis**	BDL095	KC592625	KC592909	KC593022	–	KC593128	–	KC593251	KC592492	CHILE: Region VII, Parque Nacional Altos de Lircay, Viliches Altos, 35°36′20″S 71°04′22″W, El. 1209 m, 29.i.2011, B. Lessard, D. Amorim and D. Yeates (ANIC)
			BDL110	KC592638	KC592922	KC593036	KC592802	KC593139	–	–	KC592504	CHILE: Region IV, Los Vilos, 31°53′47″S 71°30′39″W, El. 24 m, 23.i.2011, B. Lessard, D. Amorim and D. Yeates (ANIC)
			BDL111	KC592639	KC592923	KC593037	–	KC593140	–	–	KC592505	CHILE: Region IV, Los Vilos, 31°55′13″S 71°29′18″W, El. 83 m, 23.i.2011, B. Lessard, D. Amorim and D. Yeates (ANIC)
	[NZ **gen.n.**]	*adrel*	BDL101	KC592630	KC592915	KC593028	–	KC593131	–	KC593254	KC592497	NEW ZEALAND: South

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Table 1 (*continued*)

FAMILY SUBFAMILY Tribe	Genus	Subgenus	Species	Voucher ID	COIa	COIb	COII	AATS	CAD1	CAD3	CAD4	28Sfk	Collection data
				BDL102	KC592631	KC592916	KC593029	–	KC593132	–	KC593255	KC592498	Island, Canaan Rd., Abel Tasman NP, 41°00′29″S 172°53′27″E, El. 692 m, 15 Dec 2010 (ANIC)
			lerda	BDL103	KC592632	KC592917	KC593030	–	KC593133	–	KC593256	KC592499	NEW ZEALAND: North Island, East Harbour Reserve Park, 41°18′11″S 174°53′39″E, 12 Dec 2010 (ANIC)
				BDL104	KC592633	–	KC593031	–	KC593134	–	KC593257	KC592500	NEW ZEALAND: North Island, Kaimai Mamaku Forest Park, 38°01′01″S 175°57′03″E, El. 441 m, 10 Dec 2010 (ANIC)
			milleri	BDL105	KC592634	KC592918	KC593032	–	KC593135	–	KC593258	–	NEW ZEALAND: North Island, East Harbour Reserve Park, 41°18′11″S 174°53′39″E, 12 Dec 2010 (ANIC)
				BDL106	KC592635	KC592919	KC593033	–	KC593136	–	KC593259	KC592501	NEW ZEALAND: North Island, Kaimai Mamaku Forest Park, 38°01′01″S 175°57′03″E, El. 441 m, 10 Dec 2010 (ANIC)
			ricardoae	BDL107	KC592636	KC592920	KC593034	–	KC593137	–	KC593260	KC592502	NEW ZEALAND: South Island, Harwood Lookout on Route 60, 41°02′05″S 172°51′19″E, El. 751 m, 15 Dec 2010 (ANIC)
				BDL108	KC592637	KC592921	KC593035	–	KC593138	–	KC593261	KC592503	NEW ZEALAND: NEW ZEALAND: South Island, Harwood Lookout on Route 60, 41°02′05″S 172°51′19″E, El. 751 m, 15 Dec 2010 (ANIC)

according to the manufacturer's suggested reagent concentrations. Cycling conditions for 28S, COI and COII genes included an initial denaturation step at 95 °C for 5 min, followed by 33 cycles of a further denaturation at 93 °C for 20 s, annealing at 50 °C for 40 s, and elongation at 72 °C for 2 min. A final elongation at 72 °C for 5 min was allowed to complete any unincorporated bases. Cycling conditions for AATS and CAD genes included an initial denaturation at 94 °C for 4 min, followed by three cycles of: 1) five cycles of denaturation at 94 °C for 30 s, followed by annealing at 57 °C for 30 s and elongation at 72 °C for 2 min; 2) seven cycles of denaturation at 94 °C for 30 s, followed by annealing at 51 °C for 1 min and elongation at 72 °C at 2 min; 3) Repeated 37 cycles of denaturation at 94 °C for 30 s, followed by annealing at 45 °C for 20 s and elongation at 72 °C for 2 min. A final elongation of 3 min at 72 °C was allowed to include any unincorporated bases.

PCR products were visualised on 1% agarose gels using SYBR Green I Nucleic Acid Gel Stain (Invitrogen, UK) and cleaned using ExoSAP-IT® (GE Healthcare, UK) according to the manufacturer's instructions, and stored at 4 °C. Sequencing was performed using ABI (Foster City, CA) BigDye version 3 dye terminator sequencing technology and run on an ABI 3770 capillary sequencer. Sequencing PCR conditions were 40 cycles of 96 °C for 30 s, 42 °C for 15 s and 60 °C for 4 min.

2.4. Alignment and phylogenetic analysis

Nucleotide sequences were edited manually and contigs were produced for each specimen in GeneiousPro® (Drummond et al., 2011; version 5.4.6; Biomatters Ltd., available from http://www.geneious.com). Each locus was aligned independently using the Geneious Alignment and concatenated in GeneiousPro® to produce a final 5757 bp dataset (AATS; CAD regions 1, 3 and 4; COI; COII; 28S) for 176 taxa. Outgroups were chosen based on intrafamiliar and intertribal relationships with the Scionini and either sequenced or obtained from Genbank (Table 1). The general time-reversible + invariant + gamma (GTR + I + G) model was identified as the best model of substitution for each gene based on the Akaike Information Criterion (AIC) and hierarchical likelihood ratio test (hLRT) as determined by JModeltest (Darriba et al., 2012; Guindon and Gascuel, 2003; available online at http://code.google.com/p/jmodeltest2/).

For Bayesian methods, four separate analyses using four chains (set at program defaults) were performed in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) using the concatenated dataset partitioned by individual gene. Prior to running the concatenated analysis, each gene was analysed independently to confirm that the tree topology and clade monophyly was mostly congruent for all loci. Individual nuclear gene markers (AATS and CAD regions 1, 3 and 4) supported the monophyly and phylogenetic relationships of the majority of higher level taxa, including genera and subgenera, in addition to recovering the majority of species level relationships. Ribosomal 28S and the mitochondrial (COI and COII) genes recovered the majority of species level relationships, but also provided some support for the monophyly of the higher clades, although the phylogenetic relationships among these higher clades were only weakly supported. Bayesian analysis was performed on the concatenated dataset for 20 million generations, sampling every 1000 generations. A burn-in of 5 million generations (or 25% of sampled trees) was chosen as a conservative value, with the final tree showing Posterior Probabilities support for greater than 50%. Maximum likelihood (ML) analysis was performed on the same concatenated dataset online in RAxML Blackbox (Stamatakis et al., 2008; available online at http://phylobench.vital-it.ch/raxml-bb/) using a gamma model of rate heterogeneity estimating the proportion of invariable sites. The ML topology largely agreed with the Bayesian analysis, and the support values of the ML analysis were mapped onto the Bayesian tree (Fig. 2).

2.5. Divergence time estimation

A time-calibrated phylogeny was inferred by analysing a reduced subset of the concatenated dataset, limited to a single generic or subgeneric representative (BDL001, BDL005, BDL009, BDL035, BDL037, BDL039, BDL066, BDL072, BDL078, BDL082, BDL087, BDL088, BDL093, BDL097, BDL101, BDL129, BDL149, BDL155, CA2, CA6, Peleper, PEET1005, PEET1007, PEET1049, PEET1070, Philros, PLIM180, NCSU1034, NCSU1138, SAM2, SIM1000, SIM1007, SIM1151, SIM1152, SIM1171, SIM1330, SIM1337, SIM1409 and SIM1500) in the statistical software program BEAST 1.7.4 (Drummond et al., 2012, available at beast.bio.ed.ac.uk). The subfamilies of the Tabanidae were constrained as monophyletic to ensure a similar topology to the Bayesian and ML analysis described above. Two specimens of Athericidae were included in the analysis as the sister family of the Tabanidae, along with a member of the Pelechorynchidae chosen as the overall outgroup. The dataset was partitioned into two codon positions, positions (1 + 2) and 3, both with unlinked rate parameters and base frequencies across codon positions (codon partitions CP1 + 2.mu and CP3.mu priors specified as 0–1000), as well as partitioning into two separate clock models corresponding to the mitochondrial (COI and COII) and nuclear (AATS, CAD and 28S) genes each with an estimated and uncorrelated lognormal relaxed clock (both clock model partitions ucld.mean priors specified as 1.0E−5 to 1.0). The analysis was performed for 100 million generations sampling every 1000th using a GTR + I + G substitution model (with estimated base frequencies and six gamma categories) and a Yule process of speciation (commencing with a random starting tree).

A conservative normal prior of 142 MY (SD = 1) was placed on the node containing the Athericidae + Tabanidae, coinciding with the overlapping ages (144–140 MY) of the two independent and geographically dispersed fossils *E. lordi* and *L. formosus* (Section 2.2; Mostovski et al., 2003; Zhang, 2012). Additional calibration points in the form of other Tabanomorpha fossils were unused due to the limited genetic and taxon sampling of the outgroups. Moreover, the use of geological events as calibration points were omitted from the current analysis to provide unbiased divergence time estimates of the radiation of the Scionini with respect to the fragmentation of Gondwana. The resulting trees were processed in the BEAST companion program TreeAnnotator (version 1.7.4) with the burnin set to 10 million generations to produce a final consensus tree (Fig. 3).

3. Results and discussion

Phylogenetic relationships of the Tabanidae are depicted in Fig. 2. All clades are strongly monophyletic (PP > 90, BS > 75) unless otherwise stated. The Bayesian and ML analyses largely agreed with one another, with the exception of the following differences in the ML analysis: *Tabanus* sp. (BDL149) grouped as sister to *Dasybasis* (ML bootstrap value [BS] = 74; Fig. 2) instead of the *Haematopota* + *Hybomitra* + *Tabanus* clade (Bayesian posterior probability [PP] = 62); and the unsupported sister relationships of *Goniops* to the Philolichini (PP = 75), *S.* (*Scaptia*) *subcana* + *S.* (*Scaptia*) *lata* species groups to *S.* (*Myioscaptia*) + *S.* (*Plinthina*) (PP = 74), the main Australian *S.* (*Scaptia*) clade to *Fidena* + *Pityocera* (PP = 51), and the deeper node containing the majority of Australian and South American Scionini clades, excluding

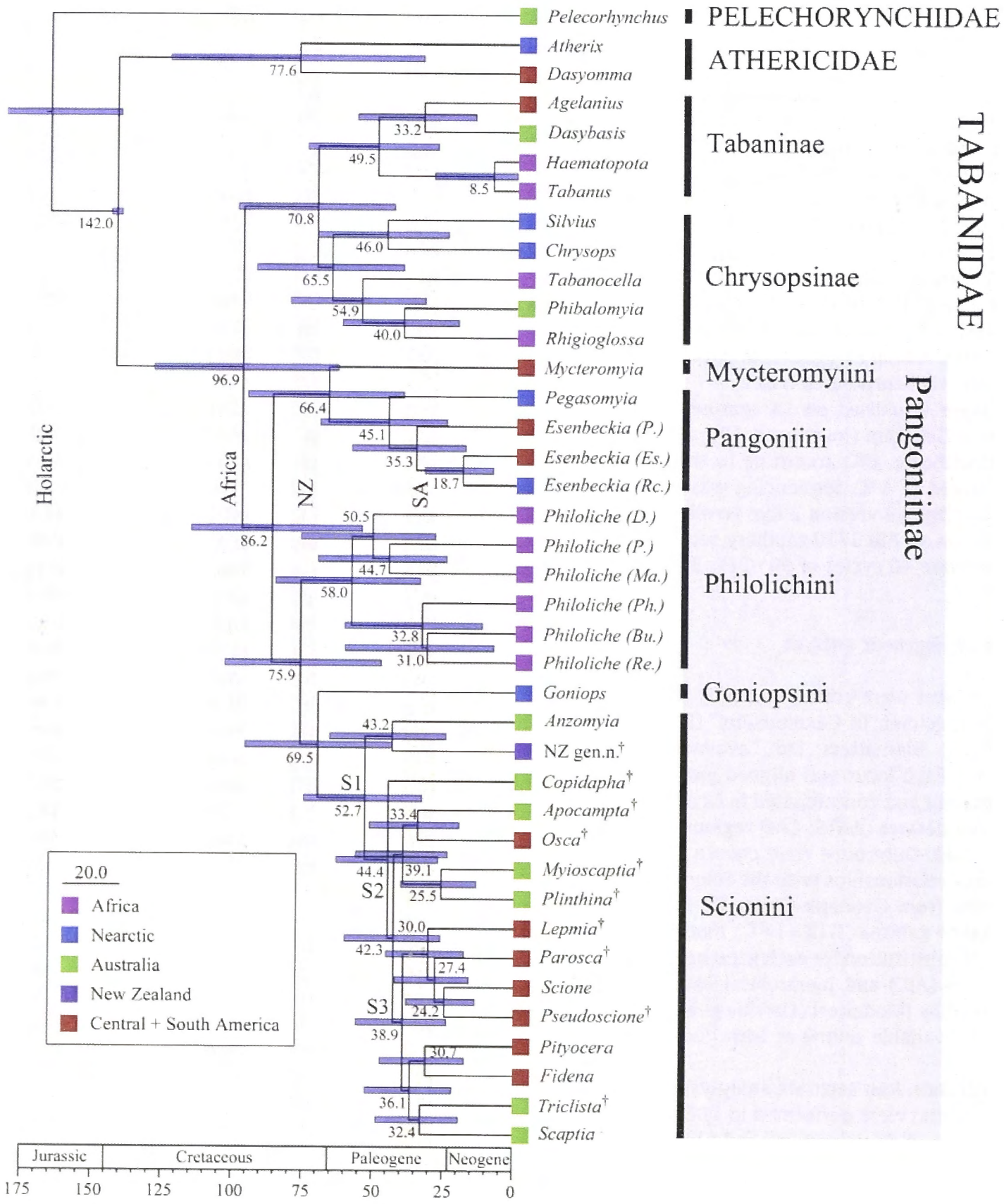

Fig. 3. Bayesian divergence time estimation of the Tabanidae. The oldest known horse fly fossils *Eotabanoid lordi* Mostovski et al., 2003 and *Laiyangitabanus formosus* Zhang, 2012 were used to conservatively constrain the node containing the Athericidae + Tabanidae (normal prior 142 MY, 1 SD; GTR + I + G; 100 million generations; CP (1 + 2), 3; mtDNA, nucDNA). The continental fragmentation of Gondwana is displayed by the vertical colour bars. †indicates the newly revised genera that previously belonged to the genus *Scaptia*. NZ, New Zealand; SA, South America.

Anzomyia and *S.* (*Pseudoscione*) from Australia and New Zealand (PP = 77).

The monophyly of the Tabanidae subfamilies were strongly supported in both the Bayesian and ML analyses of the molecular data, including the Chrysopsinae (PP = 79, BS = 46; Fig. 2), Tabaninae (PP = 100, BS = 98) and the Pangoniinae (PP = 100, BS = 100). This is reinforced by the previous molecular studies of Wiegmann et al. (2000) and Morita (2008), who also demonstrated the strong monophyly of the subfamilies of the Tabanidae. Unfortunately, the subfamily Scepsidinae has yet to be included in any molecular analysis of the Tabanidae. The inclusion of the Scionini confirms the placement of the tribe within a strongly supported monophyletic Pangoniinae.

3.1. Monophyly of the Pangoniinae tribes

The Pangoniini was strongly supported as monophyletic (PP = 100, BS = 100; Fig. 2) and sister to the Mycteromyiini (PP = 100, BS = 100). Both tribes were strongly supported as sister to the remainder of the Pangoniinae (PP = 100, BS = 100). The Philolichini was also strongly supported as monophyletic (PP = 100, BS = 100), corroborating the results of Morita (2008). The Scionini recovered as a robust monophyletic tribe (PP = 100, BS = 99), with the exclusion of the unusual monotypic genus *Goniops*; this unique genus was firmly separated from the Scionini in both analyses (PP = 100, BS = 97), and recovered as sister to the Philolichini in the Bayesian analysis only (PP = 75). This is unsurprising given

the large geographical disjunction between *Goniops* and other Scionini (eastern United States of America vs. the Southern Hemisphere; Fig. 1). The unique morphological features of *Goniops*, including the bare eyes, widened frons of females, extremely reduced proboscis and cylindrical palpi, further differentiates the genus from the remainder of the Scionini. These molecular results, combined with the distinct morphology of the genus, advocate the removal of *Goniops* from the Scionini (hereby defined to exclude *Goniops*, and therefore a robust monophyletic tribe) and its placement into a novel tribe, i.e. Goniopsini, since it does not fall within one of the existing tribes and the phylogenetic placement of the genus is dependent on the method of phylogenetic inference.

3.2. Paraphyly within Scaptia

The most widely distributed genus *Scaptia* was radically paraphyletic and comprised 11 well-supported monophyletic subclades (Fig. 2). Moreover, the South American genera *Fidena*, *Pityocera* and *Scione* recovered within the genus *Scaptia* and only two of the subgenera of *Scaptia*, *Myioscaptia* + *Plinthina*, formed a strongly supported clade (PP = 100, BS = 100). The subgenus *Scaptia* (*Lepmia*) grouped as sister to the South American clade containing *Scione*. The subgenus *Scaptia* (*Scaptia*) was also paraphyletic and formed four highly supported clades, corresponding to *Scaptia* (*Scaptia*) *subcana*, *Scaptia* (*Scaptia*) *lata*, *Scaptia* (*Scaptia*) *guttata* + *singularis*, and the major Australian *Scaptia* (*Scaptia*) clade which was sister to the South American genera *Fidena* + *Pityocera*. This was also the case for the subgenus *Scaptia* (*Pseudoscione*), which recovered as paraphyletic and was divided into four distinct clades, corresponding to species from New Zealand, Australia, and two South American clades. Unfortunately, the backbone support for the Scionini was somewhat weak in both analyses. Using the proposed cut off values of PP > 90, BS > 75, there are nine well-supported clades of Scionini discussed further below.

3.3. Resurrection of previously synonymised genera in Scaptia

In order to assess the paraphyly within *Scaptia*, type species belonging to either the current subgenera or previously synonymised genera were sequenced and included in the analysis. Results indicated that the four divisions of the paraphyletic subgenus *Scaptia* (*Scaptia*) correspond to *Scaptia sensu stricto* (type species *aurata*, Australia), and the previously synonymised genera *Apocampta* Schiner, 1867 (type species *subcana*, Australia), *Osca* Walker, 1850 (type species *lata*, South America) and *Triclista* Enderlein, 1922 (type species *singularis*, Australia). Similarly, the four divisions of the paraphyletic subgenus *Scaptia* (*Pseudoscione*) correspond to *Pseudoscione sensu stricto* (the clade containing *vitatta* + *australis* + *dorsoguttata*, South America), the previously synonymised genera *Copidapha* Enderlein, 1922 (type species *roei*, Australia) and *Parosca* Enderlein, 1922 (type species *viridiventris*, South America), as well as a putative novel genus of New Zealand species (*adrel*, *milleri*, *lerda* and *ricardoae*), hereby referred to as NZ gen.n. In addition, sampling of the type species of the *Scaptia* subgenera *Myioscaptia* (type species *violacea*, Australia) and *Plinthina* (type species *binotata*, Australia) indicate the firm separation of these subgenera from *Scaptia sensu stricto*.

The nine well supported clades (formed when applying the strict cut off values mentioned above) correspond to: (1) *Anzomyia* + NZ gen.n.; (2) *Copidapha*; (3) *Apocampta*; (4) *Osca*; (5) *Myioscaptia* + *Plinthina*; and a larger clade consisting of (6) *Triclista*; (7) *Lepmia* + *Scione* + *Parosca* + *Pseudoscione*; (8) *Pityocera* + *Fidena*, and finally; (9) *Scaptia* (Fig. 2). The paraphyly of *Scaptia* is unsurprising given that the subgenera are weakly diagnosed on the combination of few morphological characters. The molecular results suggest that the resurrection of the previously synonymised genera will correct the paraphyly within *Scaptia* and advocate the resurrection of the following genera of Scionini; *Apocampta*, *Copidapha* and *Triclista* from Australia, and *Osca* and *Parosca* from South America. The distinct monophyly in the molecular analyses also supports raising the subgenera of *Scaptia* to genus level, specifically *Lepmia*, *Myioscaptia*, *Plinthina*, and *Pseudoscione*, as well as the inclusion of a putatively novel genus, NZ gen.n. A formal taxonomic revision of the Scionini is in preparation.

3.4. Congruence with morphological evidence

The molecular phylogeny of the Scionini largely confirms the morphological classification of the tribe, however, this new molecular evidence necessitates the resurrection of several genera previously reduced to synonymies of *Scaptia*. *Anzomyia* and NZ gen.n. are distinguished from other Scionini by the dark hairy appearance, frons usually diverging at base, and short, thick proboscis. *Copidapha* also possess a narrow and strongly diverging frons, however, the proboscis is considerably longer, exceeding one and a quarter times the height of the head. Despite the modest nodal support for monophyly (PP = 71, BS = 83), Australian *Apocampta* and South American *Osca* share sabre-like palpi, a short and thick proboscis with expansively developed labella, and an elongate oblong-shaped abdomen, usually with dense lateral tufts of hairs. In contrast, the strongly supported clade of individually distinctive genera *Myioscaptia* + *Plinthina* (PP = 100, BS = 100) are distinguished by relatively few generalised characters, such as a narrow, parallel frons, relatively short and thick proboscis, and extensively broad, flattened and rounded palpi.

The remaining genera are all robustly built flies with relatively thick and stout abdomens. The Australian genera *Triclista* and *Scaptia* generally share truncated faces, short and thick proboscis with well-developed labella, and large sabre-like palpi, as it is unsurprising that *Triclista* was previously synonymised under *Scaptia* given the modest differences of the larger size and closure of the wing cells R_5 and M_3. Despite an absence in monophyly, the South American genera *Parosca*, *Pseudoscione*, *Scione*, *Pityocera* and *Fidena* are morphologically similar and united by the snout-like faces, along with the elongated and slender proboscis with reduced labella. *Scione* is distinguished from *Parosca* and *Pseudoscione* by the usually tapered palpi and wings with closure of the cells R_5 and M_3, with *Parosca* and *Pseudoscione* sharing shorter, broader palpi and wings with open cells R_5 and M_3. Both *Fidena* and *Pityocera* are linked through the strongly projecting and obviously shining faces, and an extremely long and slender proboscis that exceeds at least one and a half times the length of the head, with extremely reduced labella.

The newly resurrected genera are also supported by morphology. Australian *Copidapha* is distinguished from all other members of the Scionini by the combination of the truncate to moderately bulging face, frons moderately diverging at base, and long and slender proboscis with small labella. *Apocampta* is distinguished by the smaller size, narrowed abdomen without obvious lateral fringes of hair and black radially stained wings. In contrast, *Osca* is separated from the former genus by the larger size, broad build, abdomen with dense lateral fringes of hair and wings without obvious staining. The closely related clade of *Parosca* + *Pseudoscione* has been divided into the two separate genera, since each contain a unique type species and distinct morphological differences; *Parosca* is diagnosed by the broader build and larger extensively flattened palpi, whereas *Pseudoscione* possess short and thick palpi with a prominent bare lateral concavity. Finally, the putative novel genus from New Zealand can be distinguished from other members of the Scionini by the combination of the narrow and diverging frons, short proboscis, and large, slender palpi that are tapered and often dorsally rotated with a conspicuous lateral bare area.

Further studies are needed to determine if these morphological characters are useful in a phylogenetic context.

3.5. Evolution of the Tabanidae

The topology of the divergence time estimation tree (Fig. 3) largely agreed with the Bayesian and ML analyses (Fig. 2), with the following exceptions: *Goniops* weakly grouped as sister to the Scionini as found in the ML analysis (PP = 73); within the South American clade supported in all analyses (*Lepmia* + *Parosca* + *Scione* + *Pseudoscione*), *Pseudoscione* was sister to *Scione* (PP = 92) instead of *Parosca* as in Fig. 2; and the Australian genera *Triclista* and *Scaptia* formed a well-supported clade (PP = 98).

Divergence time estimates revealed that the subfamilies of the Tabanidae originated at 96.9 MY in the late Cretaceous (Fig. 3), forming two distinct clades corresponding to the Pangoniinae and Chrysopsinae + Tabaninae. Following this, the Chrysopsinae and Tabaninae diverged at 70.8 MY in the late Cretaceous/early Paleogene. This is somewhat older than the 57 MY split between the Chrysopsinae and Tabaninae estimated in the time-calibrated tree of all Diptera by Wiegmann et al. (2003). This previous study, however, was limited to two individuals representing each subfamily and used only a single fragment of the 28S gene. In the present study, the tribes of the Pangoniinae began to diversify at 86.2 MY with the formation of two main clades of Mycteromyiini + Pangoniini and Philolichini + Scionini + *Goniops*. The Mycteromyiini and Pangoniini separated at 66.4 MY and the Pangoniini crown began to diversify at 45.1 MY, with the tribes contemporary genera and subgenera formed by 18.7 MY. Finally, the tribe Philolichini diverged from *Goniops* + Scionini at 75.9 MY during the late Cretaceous.

3.6. Biogeography of the Pangoniinae

The global radiation patterns of the Pangoniinae can be assessed by corroborating the results of the divergence time estimation with the timing of the sequential breakup of the ancient supercontinent Gondwana. The Nearctic clades in the analysis, including *Goniops*, *Pegasomyia*, *Esenbeckia* (*Rc.*) and *Silvius* + *Chrysops*, arose between 69.5 and 18.7 MY (Fig. 3). This was well after the fragmentation of Laurasia from Gondwana which occurred at 180–160 MY (Sanmartín and Ronquist, 2004) when the Pelecorhynchidae, Athericidae and Tabanidae still all shared a common ancestor. These recent diversification dates of the Tabanidae from the Nearctic suggest that the Holarctic was more recently colonised, most likely via long distance dispersal of South American ancestors migrating along the volcanic islands that eventually formed the Central American Peninsula by 23–14 MY (Kirby et al., 2008). Similarly, African members of the *Philoliche* diversified from the Scionini at 75.9 MY. This was nearly 20 MY after the fragmentation of Africa from the remainder of Gondwana during the mid-Cretaceous at 110–95 MY (Sanmartín and Ronquist, 2004), suggesting that Africa was colonised after the separation of the continent from Gondwana, most likely via long distance dispersal. Conversely, the colonisation of Africa by the Philolichini may be alternatively explained by plausible vicariance, since the nodes confidence interval does overlap with the serration of Africa from Gondwana (102.7–47.2 MY). Furthermore, more recent divergence was exhibited in the African members of *Haematopota* + *Tabanus* and *Rhigioglossa*, suggesting mechanisms of long distance dispersal for these genera.

The Scionini appear to be a classic Gondwanan group, with Mackerras (1960, p. 7) stating "the Scionini of Australia, New Zealand and South America clearly came from a common stock, and there has been vigorous adaptive radiation in the two larger continents. Whether this was achieved by drifting continents, or by some other means, is a question that biological evidence cannot answer". The results of all three analyses revealed that *Anzomyia* + NZ. gen.n. are sister to the reminder of the Scionini (Figs. 2 and 3), a typical pattern exhibited in many Gondwanan groups where the New Zealand taxa are often sister to Australian and South American members (Crisp et al., 2011; Sanmartín and Ronquist, 2004). Divergence time estimates suggest the separation of *Anzomyia* + NZ gen.n. from the remaining Scionini (52.7 MY; S1: Fig. 3) occurred sometime after Zealandia, the ancient landmass that eventually gave rise to modern New Zealand, separated from the remainder of Gondwana at 82–70 MY during the late Cretaceous (Crisp et al., 2011; Sanmartín and Ronquist, 2004). This suggests that New Zealand was colonised more recently via long distance dispersal.

Long distance dispersal of Australian fauna to New Zealand may have been facilitated by a series of atolls similar to today's Kermadec Islands that once connected Zealandia to the rest of Gondwana. Such atolls may have been more pronounced or even connected during periods of glaciation, similar to when mainland Australia was connected to Tasmania during the recent glaciation events of approximately 9000–6500 years ago. The larvae of some Scionini genera are known to develop within close proximity to decaying tree trunks (Coscarón and González, 1989), which may have floated from Australia to New Zealand and henceforth radiated. While unusual, this hypothesis is plausible given that the larval development of horse flies can take up to 3 years to complete (Coscarón and González, 1989; English, 1955), giving time to survive such a journey. An alternative hypothesis for the colonisation of New Zealand may still be explained by vicariance, as the confidence interval of the node containing the split between *Anzomyia* + NZ gen.n. and the remainder of the Scionini overlaps with the fragmentation of Zealandia from Gondwana (74.5–32.5 MY; S1: Fig. 3). Mackerras (1957, p. 583) hypothesised that "New Zealand has been too isolated since the Pleistocene for recolonisation to have occurred, but there is enough evidence of recent speciation to suggest rehabilitation of a previously depressed fauna". Either scenario may have led to the colonisation of New Zealand, including vicariance of ancestral fauna that have since suffered an extinction event, such as the drowning of Zealandia during the Oligocene (35–24 MY), with survivors undergoing subsequent speciation, or alternatively, more recent long distance dispersal of Australian fauna to vacant niches of New Zealand with subsequent speciation. Long distance dispersal of Australian flies to New Zealand has been previously reported in the literature; a limited number of individuals of *Comptosia moretonii* Macquart, 1855 (Diptera: Bombyliidae), a predominantly south eastern Australian species, have been collected from the South Island of New Zealand and were suggested to have migrated across the Tasman Sea by wind drifting (Yeates, 1991).

The colonisation of Australia and South America by the Scionini is less obvious, as Mackerras (1955, p. 490) confirmed "it is difficult to define a precise point of division between the series". In the present molecular study it is also difficult to infer the number of sister-group splits between Australian and South American clades due to poor nodal support on the trees backbone (Fig. 2). Well supported nodes which include splits between Australian and South American taxa were dated at 44.4 (S2: Fig. 3) and 38.9 MY (S3: Fig. 3) and coincide with the fragmentation of South America from Australia at 40–28 MY ago in the Paleogene (Crisp et al., 2011; Sanmartín and Ronquist, 2004). Therefore the colonisation of Australia and South America by the Scionini was most likely due to ancient vicariance, perhaps using Antarctica as a biological corridor for migration. Furthermore, the short branch lengths exhibited in all analyses (Figs. 2 and 3) suggest that the genera rapidly radiated, possibly coinciding with the exploitation of new, previously unoccupied niche-space. These results are somewhat in accordance with the previous divergence time estimates of Cranston et al.

(2010, 2012) and Krosch et al. (2011), who independently demonstrated that the Gondwanan pattern in the current biogeography of the Chironomidae was formed by processes of both vicariance and long distance dispersal.

Mackerras (1960) hypothesised that the Scionini may have evolved in a temperate Antarctica and radiated out to New Zealand, Australia and South America. Although the Antarctic taxa are extinct, given the dominant presence of Australian clades with the South American genera nestled within, it is plausible that the Scionini are Australian in origin and subsequently radiated out into the Southern Hemisphere. Based on all analyses (Figs. 2 and 3), there appears to be at least three main waves of radiation from Australia; (1) the colonisation of New Zealand by the NZ. gen.n. lineage; (2) the radiation of the *Osca* lineage to South America; and (3) the radiation of *Lepmia* + *Parosca* + *Scione* + *Pseudoscione* and *Pityocera* + *Fidena* also to South America. Based on the unsampled taxa, there may be a possibility for two additional radiations of the Scionini from Australia, including a second more recent dispersal to New Zealand by *Anzomyia herculensis* Lessard, 2012, the only New Zealand species of *Anzomyia*, and a separate dispersal to South America by the *Pseudomelpia* lineage. Mackerras (1960) also hypothesised that the Australian Scionini colonised New Guinea more recent during the glaciation events of the Pleistocene ice age. Therefore, based on this molecular data, the Scionini are most likely Australian in origin and have radiated into New Zealand and South America via complex mechanisms of both long distance dispersal and vicariance.

4. Conclusion

This study successfully reconstructed the phylogenetic relationships of the austral horse fly tribe Scionini using multiple independent molecular markers. Molecular data have proven useful in resolving the systematic relationships of a taxonomically difficult group, despite the limited traditional morphology-based classification schemes, although some deeper nodes within the tribe still remain unclear. The genus *Scaptia* requires significant taxonomic revision as it currently comprises several subgenera which are recommended to be raised to genus level (*Lepmia*, *Myioscaptia*, *Plinthina* and *Pseudoscione*), in addition to the resurrection of several genera (*Apocampta*, *Copidapha*, *Parosca*, *Osca* and *Triclista*) which were previously reduced to synonymies of *Scaptia*. The molecular data also supported a putative novel genus endemic to New Zealand, which will be formally described in a subsequent publication. The molecular data, combined with distinct morphological evidence, supports the removal of the Nearctic genus *Goniops* from the Scionini, resulting in the exclusive Southern Hemisphere distribution of the tribe. Unfortunately, some unique taxa of the Scionini, including *Caenopangonia*, and the former *Scaptia* subgenera *Palimmecomyia* and *Pseudomelpia*, were unable to be sampled in the present molecular analyses and are desired for future genetic studies. Based on distinct morphology, *Caenopangonia* is expected to belong to the Mycteromyiini instead of the Scionini, and *Palimmecomyia* and *Pseudomelpia* are expected to represent unique genera of the Scionini.

Divergence time estimates based on the genetic data and fossil record placed global biogeographic radiations of the Pangoniinae in a temporal context. Results indicated that the Scionini are a typical Gondwanan group that most likely originated in Australia, with subsequent radiation into the Southern Hemisphere. Moreover, the current biogeography of the Scionini is explained by a dynamic process involving both plausible long distant dispersal to New Zealand and vicariant migration to South America. Future investigations should focus on more extensive sampling of the South American genera, particularly the subgenera of *Fidena* and *Pityocera*, which will aid supplementary taxonomic revisions of the tribe.

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Appendix A. Supplementary material

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Table S1: Primers used for PCR amplification and nucleotide sequencing in this study.

Gene	Primer	Sequence 5'→ 3'	Length (bp)	Reference
28S	28K	GAA GAG CCG ACA TCG AAG	18	Wiegmann *et al.* (2000)
	rc28F	GTG ATT TCT GCC CAG TGC TCT G	22	Wiegmann unpublished
AATS	SCAATS53F	GGC AAT TGG TCG TTT GGW G	19	This study
	M13rA1x244R	CAG GAA ACA GCT ATG ACC ATN CCR CAR TCN ATR TGY TT	38	Wiegmann unpublished
CAD1	CAD1-SF2	GCT AAC RTA TCC CCT RAT TGG	21	This study
	405RTab	GCN GTR TGY TCN GGR TGR AAY TG	23	Moulton & Wiegmann (2004)
CAD3	CAD3-SF1	GTA CAA TGT RAA AAT ACT TGG G	22	This study
	CAD3-SR1	CCT ACA CTT TTC ATY GAR CTW CC	23	This study
CAD4	CAD4-SF1	GCA CGW GTT TGT AAG AAY ATA GG	23	This study
	CAD4-SR1	CCA TAA CGA CTT CAA AWG	18	This study
COIa	TY-J-1460 (mtd4)	TAC AAT TTA TCG CCT AAA CTT CAG CC	26	Sperling *et al.* (1994)
	C1-N-2329	ACT GTA AAT ATA TGA TGA GCT CA	23	Simon *et al.* (1994)
COIb	C1-J-2183 (Jerry)	CAA CAT TTA TTT TGA TTT TTT GG	23	Simon *et al.* (1994)
	TL2-N-3014 (Pat)	TCC AAT GCA CTA ATC TGC CAT ATT A	25	Simon *et al.* (1994)
COII	mtd13 (J3034)	AAT ATG GCA GAT TAG TGC A	19	Liu and Beckenbach (1992)
	R Lys	GAG ACC AGT ACT TGC TTT CAG TCA TC	26	Whiting (2002)

Afterword: Chapter Seven

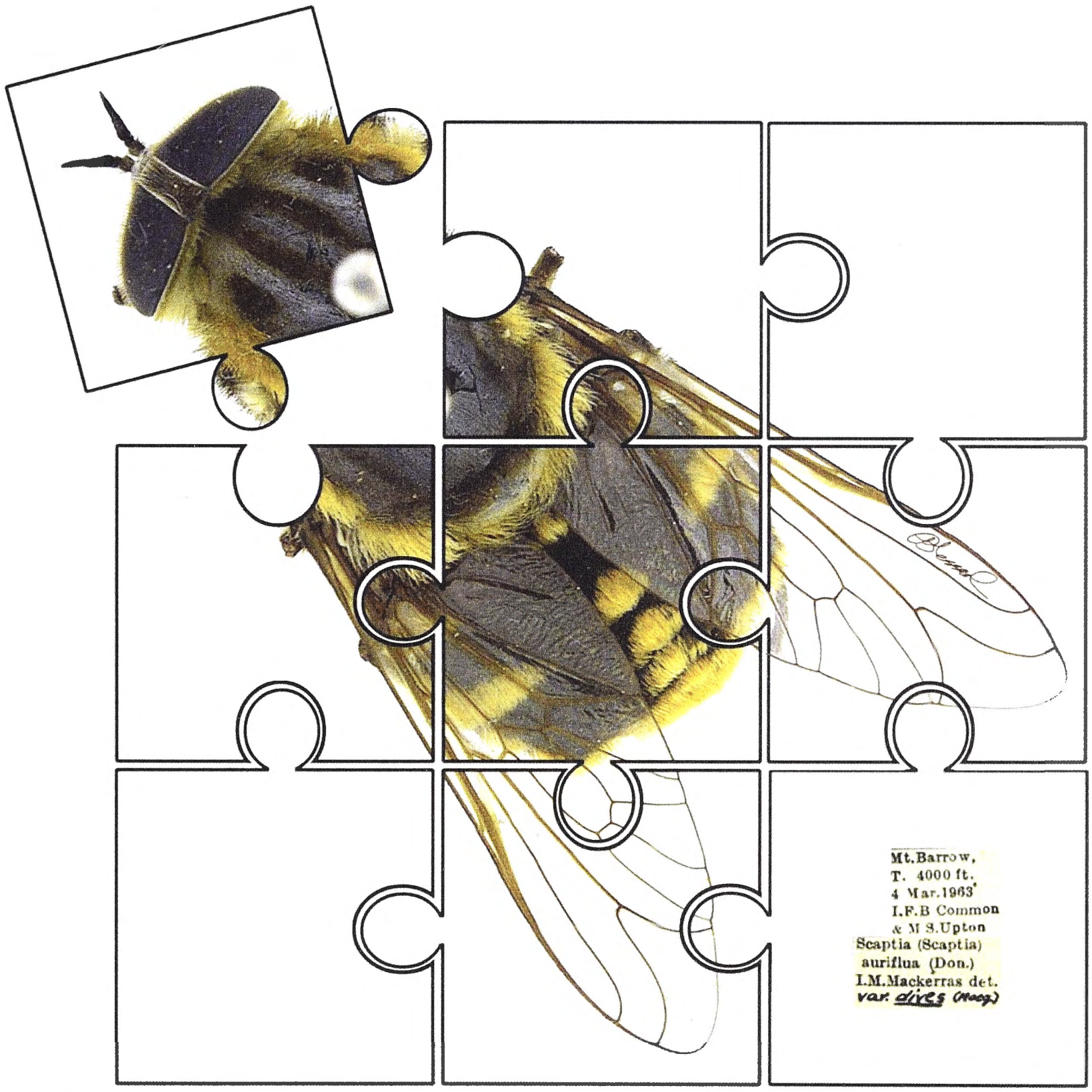
The molecular evidence presented in Chapter Seven demonstrated the utility of mitochondrial and molecular gene markers in reconstructing the phylogenetic relationships of the Scionini. The monophyly of the tribe was well-supported, including the monophyly of the genera *Fidena, Pityocera* and *Scione,* corresponding to traditional morphology-based classification schemes. The paraphyly of *Scaptia* indicated that the most widespread genus warranted taxonomic revision, including the reassessment of the subgenera and some erroneously synonymised genera. Furthermore, the molecular data also questioned the taxonomic placement of *Caenopangonia* and *Goniops* within the Scionini.

Chapter Eight aims to correct the paraphyly of *Scaptia* by using morphological evidence to validate the taxonomic changes recommended by the molecular analysis presented in Chapter Seven. These suggested changes included raising of the subgenera of *Scaptia* to genus level and resurrecting several former genera that were erroneously synonymized. In addition, a novel genus was established to satisfy the distinct monophyly of the New Zealand clade that recovered as sister to *Anzomyia* Lessard, 2012**.** Morphology will also be used to redescribe all Scionini genera and will provide more robust taxonomic concepts for the genera, especially since many have previously suffered from inadequate original descriptions. Similarly, morphological evidence will also validate the removal of *Caenopangonia* and *Goniops* from the Scionini as proposed in Chapter Seven. A novel diagnostic key to the tribe will also be developed for the first time to accommodate all seventeen recognised genera of Scionini.

Chapter Eight

Revision of the austral horse fly tribe Scionini (Diptera: Tabanidae)

Bryan D. Lessard



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Chapter Eight

Revision of the austral horse fly tribe Scionini (Diptera: Tabanidae)

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Abstract

The hairy-eyed horse fly tribe Scionini comprises over 280 species and are austral in distribution, occurring in Australia, New Guinea, New Zealand and South America. Most adult females are blood-feeding and can transmit multiple diseases to humans and animals, although both sexes are important pollinators of many plants. The current taxonomy of the tribe is hindered by the limited availability of reliable diagnostic characters, as many genera are often weakly diagnosed by combinations of few morphological characters. Recently, the first quantitative phylogenetic hypothesis for the Scionini was provided using molecular data to demonstrate the well-supported monophyly for the tribe, although the widespread genus *Scaptia* recovered as wildly paraphyletic and formed a series of monophyletic clades corresponding to either subgenera or previously synonymised genera. This present study formally revises and validates the genera of the Scionini, focusing on the most widespread genus *Scaptia*. All genera are redescribed, illustrated and included for the first time in an updated diagnostic key to the genera of the tribe. The Scionini are now defined to include seventeen genera corresponding to previously standing genera (*Anzomyia* Lessard, 2012, *Fidena* Walker, 1850, *Pityocera* Giglio-Tos, 1896, *Scaptia* Walker, 1850, and *Scione* Walker, 1850), newly revised genera (*Lepmia* Fairchild, 1969 **stat.n.**, *Myioscaptia* Mackerras, 1955 **stat.n.**, *Palimmecomyia* Taylor, 1917 **stat.n.**, *Plinthina* Walker, 1850 **stat.n.**, *Pseudomelpia* Enderlein, 1922 **stat.n.** and *Pseudoscione* Lutz, 1918 **stat.n.**), newly resurrected genera (*Apocampta* Schiner, 1867 **stat.n.**, *Copidapha* Enderlein, 1922 **stat.n.**, *Parosca* Enderlein, 1922 **stat.n.**, *Osca* Walker, 1850 **stat.n.**, and *Triclista* Enderlein, 1922 **stat.n.**) and a novel genus from New Zealand (*Aotearomyia* Lessard, **gen.n.**). The

two morphologically distinct genera *Caenopangonia* Kröber, 1930 **trans.n.** and *Goniops* Aldrich, 1892 **trans.n.** have also been removed from the Scionini and reassigned to the more appropriate tribes Mycteromyiini and Goniopsini Lessard **tribe.n.**, respectively.

Keywords. Mackerras, Pangoniinae, phylogenetics, *Scaptia*, systematics.

Introduction

The Tabanidae, commonly referred to as horse, deer or march flies, are a cosmopolitan family of Diptera with over 4400 species currently described (Pape & Thompson 2012). Both males and females are vital pollinators of many plants, feeding on the nectar of Australian *Eucalyptus, Grevillea* and *Melaleuca,* in addition to *Leptospermum* in Australia and New Zealand, and *Luma* in South America (Johnson & Morita 2006; Lessard & Yeates 2012b; Mackerras 1957, 1960; Morita 2008; Tillyard 1926). The family also exhibits sexually dimorphic feeding habits, as adult females are known blood-feeders and can mechanically transmit several disease-causing microbes in cattle, horses, macropods and even humans (Foil 1989; Foil *et al.* 1984, 1988; Krinsky 1976; Scoles *et al.* 2008; Spratt 1972a, 1972b, 1974a, 1974b, 1975; Reid *et al.* 2001). Therefore, the Tabanidae have considerable medical and ecological importance.

The classification of the Tabanidae

A recent surge of renewed taxonomy has expanded the knowledge of the Australasian Tabanidae (Lessard & Yeates 2011, 2012a, 2012b, 2013; Lessard *et al.* 2013; Mackerras *et al.* 2008). The monophyly of the Tabanidae is well-supported by both morphological (Mackerras 1954; Yeates 2002) and molecular evidence (Lessard *et al.* 2013; Morita 2008; Wiegmann *et al.* 2000, 2011). Based on the innovative morphological work of Mackerras (1955), the Tabanidae are currently recognised as comprising four subfamilies, with further division into one or more tribes; Chrysopsinae (Bouvieromyiini, Chrysopsini and Rhinomyzini), Pangoniinae (Mycteromyiini, Goniopsini Lessard **tribe.n.**, Pangoniini, Philolichini and Scionini), Scepsidinae, and Tabaninae (Diachlorini, Haematopotini and Tabanini).

Chapter Eight

The austral tribe Scionini

The tribe Scionini, from the subfamily Pangoniinae, are formed of mostly stout, bearded and hairy-eyed flies. Previous to this study, the tribe was recognised to consist of seven genera, with some being further divided into subgenera, including *Caenopangonia* Kröber, 1930 **trans.n.**, *Fidena* Walker, 1850, *Goniops* Aldrich, 1892 **trans.n.**, *Pityocera* Giglio-Tos, 1896, *Scaptia* Walker, 1850, *Scione* Walker, 1850 and the most recently described genus *Anzomyia* Lessard, 2012. With the exception of the monotypic Nearctic genus *Goniops* (Brennan 1935; Mackerras 1955), the Scionini are predominantly austral in distribution, occurring in Australia, New Guinea, New Zealand and South America (Lessard & Yeates 2012a, 2012b; Mackerras 1955, 1960). Moreover, *Goniops* and *Caenopangonia* notably differ in morphology and are distinguished from the remainder of Scionini, as both genera presence bare eyes in both sexes and an extremely widened frons in females.

The genus *Scaptia* is the most species-rich and widest spread of the Scionini, occurring in Australia, New Guinea, New Zealand and South America. The genus was traditionally divided into seven subgenera, including *Lepmia* Fairchild, 1969 **stat.n.** (found in Brazil), *Pseudomelpia* Enderlein, 1922 **stat.n.** (Chile), *Myioscaptia* Mackerras, 1955 **stat.n.** (Australia), *Palimmecomyia* Taylor, 1917 **stat.n.** (Australia), *Plinthina* Walker, 1850 **stat.n.** (Australia), *Scaptia* Walker, 1850 (Australia, Chile, Peru, Bolivia, Argentina), and *Pseudoscione* Lutz, 1918 **stat.n.** (Australia, Argentina, Brazil, Chile, New Guinea and New Zealand).

Challenges of traditional taxonomy

The taxonomy of the Scionini has been historically challenging given the difficulties associated with the morphological uniformity of most genera. As a result, genera are often weakly diagnosed by the combination of relatively few morphological characters that are not necessarily useful or informative when applied to other groups. These main diagnostic characters include the ratio of the frons (calculated by dividing the length of the vertex to the top of the subcallus by the width of the midlength of the frons); the bulging or truncated form of the face; the length and width of the palpi and form of the lateral sensory pit; the length and width of the proboscis; and the closure of the wing cells R_5 and M_3

(Mackerras 1955, 1960). Genitalia are usually neglected in diagnoses for genera and species, as large structural differences in the genitalia do not correspond to differences in external morphology and therefore cannot often aid in species identification (Mackerras 1955, 1960).

Mackerras (1955, p. 455) further lamented "the situation is further complicated by the large number of species in the family, repeated evolution, paucity of structural characters, and the fact that segregates are quite distinct in one region but merge together in another, so that workers in different regions would naturally have different opinions about their validity". The taxonomy of the tribe is somewhat fragmented due to the historically disjointed efforts by previous workers, with conflicting taxonomic changes that are published in a myriad of languages such as English, German and Spanish. This is especially the case for the South American genera that have been considered to be in a "chaotic condition" (Fairchild 1956, p. 9). Moreover, many original descriptions for the genera of the Scionini are often inadequate or incomplete; Enderlein (1922) and Lutz *et al.* (1918) introduced several novel genera (*Pseudomelpia* and *Pseudoscione*, and the previously synonymised genera *Copidapha* Enderlein, 1922 **stat.n.**, *Parosca* Enderlein, 1922 **stat.n.**, and *Triclista* Enderlein, 1922 **stat.n.**) in either a rudimentary taxonomic key or mere checklist of species, without a formal taxonomic description and little systematic context. Many international workers have also broadly applied the genus *Scaptia* to the majority of Australian, New Zealand and South American species of Scionini.

Consequently, many genera of the Scionini have been questionably synonymised in the past due to the poor understanding of their taxonomy and systematic relationships. For example, the genera *Apocampta* Schiner, 1867 **stat.n.** and *Osca* Walker, 1850 **stat.n.** were reduced to synonyms of *Scaptia* by Ferguson (1924, 1926), based on the few similarities of the parallel frons, long, narrow and sabre-like palpi, and short and thick proboscis. Similarly, *Triclista* was reduced to a synonym of *Scaptia* by Ferguson (1926) who neglected the modest morphological differences of the larger size and closure of the wing cells R_5 and M_3. Finally, the well-dispersed genera *Parosca* (from South America) and *Copidapha* (Australia) were also reduced to synonomies of the subgenus *Scaptia* (*Pseudoscione*) by Ferguson (1926) and Mackerras (1955), based on the few similarities of the diverging frons, long and slender proboscis, and short and thick palpi.

Despite these historical challenges, the recent study of Lessard *et al.* (2013) demonstrated the utility of molecular data to successfully reconstruct the evolutionary relationships of the Scionini (solid branches in Figure 1). All clades in this previous phylogenetic analysis included the type species of the majority of the genera, subgenera and previously synonomysed genera of the Scionini, with the exception of some taxa (*Anzomyia, Fidena, Lepmia, Pityocera, Pseudoscione* and *Scione*). Using several mitochondrial (COI and COII), ribosomal (28S) and nuclear (AATS and CAD regions 1, 3 and 4) gene markers, Lessard *et al.* (2013) provided the first robust molecular phylogenetic hypothesis for the Scionini and demonstrated the well-supported monophyly of the tribe (Bayesian inference posterior probability [PP] = 100, maximum likelihood bootstrap support [BS] = 99; Lessard *et al.* 2013), including the well-supported monophyly for the South American genera *Fidena* (PP = 100, BS = 99), *Pityocera* (PP = 100, BS = 100) and *Scione* (PP = 99, BS = 100). Conversely, the widespread genus *Scaptia* recovered as radically parapyletic, indicating that major taxonomic revision was warranted for the genus which formed several well-supported monophyletic clades corresponding to: several subgenera of *Scaptia*, including *Lepmia* (PP = 97, BS = 94), *Myioscaptia* (PP = 100, BS = 100), *Plinthina* (PP = 100, BS = 99), and *Pseudoscione* (PP = 100, BS = 97); a novel genus *Aotearomyia* Lessard, **gen.n.** (PP = 100, BS = 100) from New Zealand (described herein), and; several genera which were previously synonomysed, including *Apocampta* (PP = 100, BS = 98), *Copidapha* (PP = 89, BS = 79), *Parosca* (PP = 100, BS = 100), *Osca* (PP = 100, BS = 100) and *Triclista* (PP = 100, BS = 100). Moreover, the distinct molecular monophyly identified these latter taxa as valid genera of the Scionini which were erroneously reduced to synonyms of the genus *Scaptia*. Interestingly, the bare-eyed Nearctic genus *Goniops* was firmly separated from the Scionini (PP = 100, BS = 99), and recovered as sister to either the Scionini or Philolichini depending on the phylogenetic method of inference (Lessard *et al.* 2013). Therefore, the taxonomic placement of *Goniops* remains uncertain.

The reported paraphyly within *Scaptia* and incorrect synonomy of several genera of the Scionini is unsurprising given the limited use of morphological characters by previous workers. This study formally revises and validates the genera of the Scionini under extensive morphological examination, with a particular focus placed on the well-dispersed genus *Scaptia*. All genera have been redescribed, illustrated, and provided with

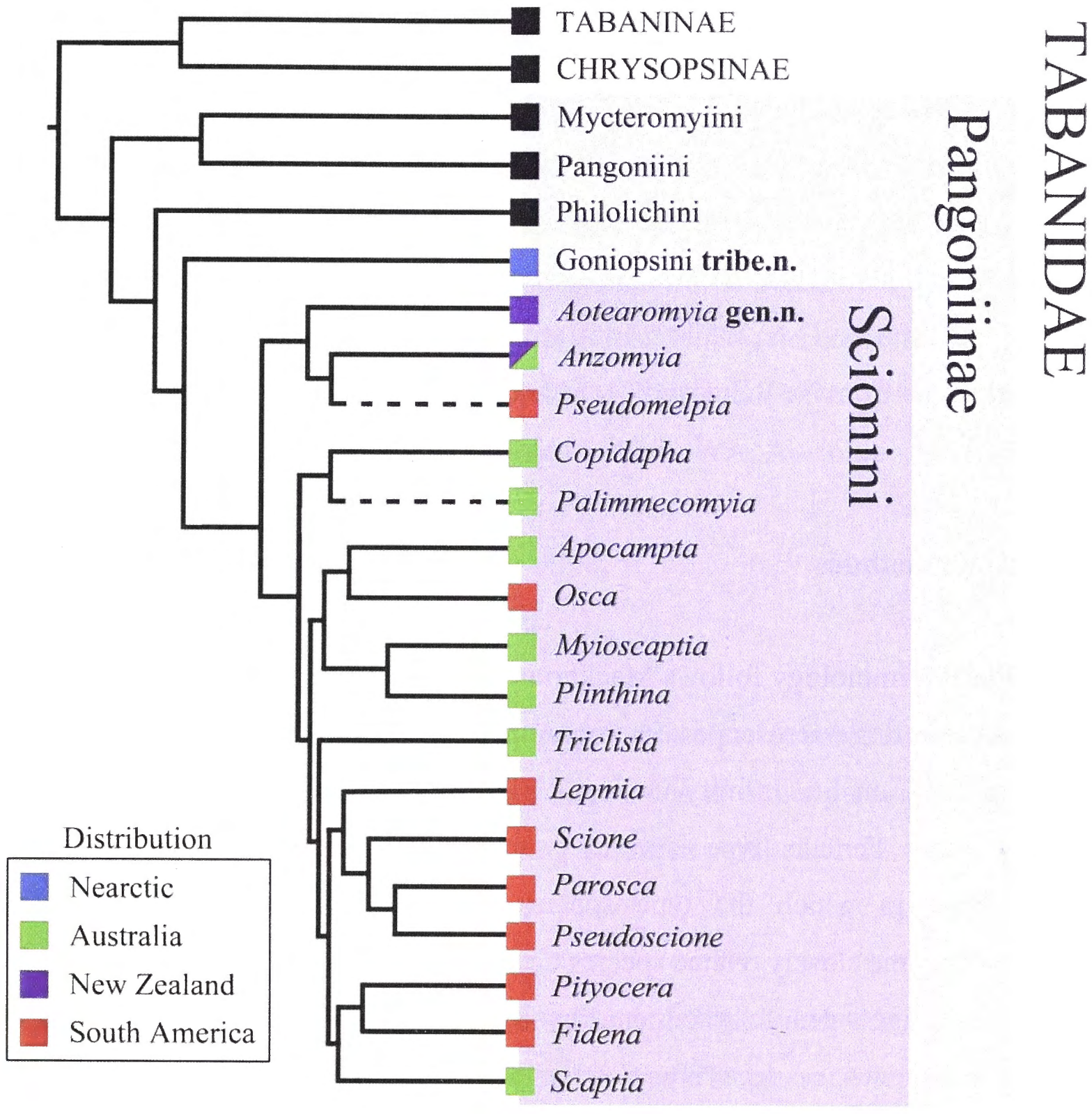

Figure 1: Phylogenetic relationships of the austral horse fly tribe Scionini inferred from molecular data (Lessard *et al.* 2013; solid branches) and qualitative morphology (dashed branches).

information regarding the number of described species (presented in Species List), distribution, feeding habits, and larval stages if known. Morphological characters were also used to qualitatively infer the phylogenetic position of the genera *Palimmecomyia* and *Pseudomelpia* (Figure 1), which are absent in the current molecular-based phylogenetic hypothesis for the tribe. The distinct genera *Caenopangonia* Kröber, 1930 **trans.n.** and *Goniops* Aldrich, 1892 **trans.n.** have since been removed from the Scionini and are reassigned to the tribes Mycteromyiini and Goniopsini Lessard, **tribe.n.**, respectively, with the latter described herein. The classification scheme for Pangoniinae is updated for the first time since Mackerras (1955) revision of the subfamily and a novel diagnostic key for the Scionini is also provided to include all recognised genera of the tribe. The tribe Scionini is hereby defined to include seventeen genera, corresponding to

previously standing genera (*Anzomyia* Lessard, 2012, *Fidena* Walker, 1850, *Pityocera* Giglio-Tos, 1896, *Scaptia* Walker, 1850 *sensu stricto*, and *Scione* Walker, 1850), newly revised genera (*Lepmia* Fairchild, 1969 **stat.n.**, *Myioscaptia* Mackerras, 1955 **stat.n.**, *Palimmecomyia* Taylor, 1917 **stat.n.**, *Plinthina* Walker, 1850 **stat.n.**, *Pseudomelpia* Enderlein, 1922 **stat.n.** and *Pseudoscione* Lutz, 1918 **stat.n.**), newly resurrected genera (*Apocampta* Schiner, 1867 **stat.n.**, *Copidapha* Enderlein, 1922 **stat.n.**, *Parosca* Enderlein, 1922 **stat.n.**, *Osca* Walker, 1850 **stat.n.**, and *Triclista* Enderlein, 1922 **stat.n.**), and a novel genus from New Zealand (*Aotearomyia* Lessard, **gen.n.**).

Materials and methods

Morphological terminology follows Mackerras *et al.* (2008). Specimens were examined using Zeiss dissecting microscopes. Photographs were acquired on a BK Plus Lab System featuring aP-51 Cam lift, Infinity Optics K2 Long Distance Microscope, and Helicon Focus software. Female type species were imaged for all genera, excluding *Caenopangonia* in which the type species was unavailable for imaging and is supplemented by the closely related species *Caenopangonia brevirostris* (Philippi, 1865). Asterisks and daggers denote specimens physically examined by the author and the type species of each genus, respectively. Novel type material is deposited at the Australian National Insect Collection (ANIC), Canberra, Australia.

All examined material was sourced from the following institutions:

AM	Australian Museum, Sydney, NSW, Australia
ANIC	Australian National Insect Collection at CSIRO Ecosystem Sciences, Canberra, ACT, Australia
BYU	Brigham Young University, Utah, USA
ERM-LUNZ	Entomology Research Museum, Lincoln University, Canterbury, New Zealand
GDCD	Greg Daniels Private Collection, Brisbane, Qld, Australia (now integrated into AM and QM)
MNZ	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand
NCSU	North Carolina State University, Raleigh, North Carolina, USA

NMH	The Natural History Museum, London, United Kingdom
QDPI	Queensland Department of Primary Industries, Indooroopilly, Qld, Australia
QM	Queensland Museum, Brisbane, Qld, Australia
UQIC	University of Queensland Insect Collection, Brisbane, Qld, Australia
USP	University of São Paulo, Ribeirão Preto, Brazil
SAM	South Australian Museum, Adelaide, SA, Australia
SI	Smithsonian Institute, Suitland, Maryland, USA
WAM	Western Australian Museum, Perth, WA, Australia

Subfamily PANGONIINAE Loew, 1860

Morphological diagnosis. Mostly stoutly built flies with relatively long and slender legs, with short to remarkably long proboscis, either rotund to rather parallel sided, elongated or narrowed bodied. Frons usually diverging but often parallel, and without a prominent callus.

Mackerras (1955, p. 456) adequately described the subfamily as: "ninth tergite an undivided chitonous shield in males; almost always a single transverse bar in females. Ocelli well-developed (except in African genera). Antennae short, little if at all longer than the antero-posterior diameter of the head; scape and pedicel short; flagellum usually subulate, sometimes with basal annuli swollen, usually 6-8 annulate. Hind tibiae with paired apical spurs (sometimes minute, occasionally not detectable). Vein *sc* bare above and below. Style of male hypopygium single or bifid, finger-like or pointed. Caudal ends of spermathecal ducts of female without mushroom-like expansions".

A revised key to tribes of the Pangoniinae subfamily

1. Eyes nearly always hairy; ocelli present. Wing vein R_4 with a variable appendix, usually absent (Figures 2-18). Australasian and Neotropical..... Scionini Enderlein, 1922

Eyes usually bare; ocelli present or absent. Wing vein R_4 nearly always with a strong appendix. Asian, Ethiopian, Palaeartic, Nearctic, Neotropical, Australasian..... 2

2. Ocelli absent (excluding *Buplex* Austen, 1920). Gonopophyses of female widely separated, and the distal edge of the eighth sternite strongly chitinised. Asian, northern Australasian, Ethiopian..... Philolichini Mackerras, 1954

Ocelli present. Gonopophyses of female not widely separated. Palaeartic, Nearctic, Neotropical, Australasian..... 3

3. Style of male hypopygium always finger-like. Frons always exceedingly wide (frons index 1). Face extremely truncated. Proboscis conspicuously short and less than the head length (Figure 19). Nearctic..... Goniopsini Lessard, **tribe.n.**

Style of male hypopygium always bifid. Frons either wide or narrowed. Face moderately truncate or conically produced. Proboscis usually long and exceeding the head length, occasionally equal to length of head. Palaeartic, Nearctic, Neotropical, Australasian..... 4

4. Antennal flagellum often with basal flagellomeres swollen or fused. Frons almost always narrow (index never approaching 1, excluding *Therevopangonia* Mackerras, 1955), rarely covered in dense hairs, usually with a distinct subcallus. Face truncate to moderately bulging. Palaeartic, Nearctic, Neotropical, Australasian..... Pangoniini (Loew, 1860)

Antennal flagellum with 8 distinct and unswollen flagellomeres. Frons wide (index approaching 1), covered in dense hairs, subcallus indistinct. Face usually conical to snout-like (Figure 20). Neotropical..... Mycteromyiini Coscarón & Philip, 1979

Distribution. The subfamily has a near global radiation, occurring in Australasia, Asia, Africa, Europe, and North, Central and South America (Mackerras 1955).

Tribe SCIONINI Enderlein, 1922

Morphological diagnosis. The Scionini are small to large (length 6-24 mm), stoutly built and hairy flies with well-defined ocelli, and hairy eyes that are always holoptic in males. Face either truncate, bulging or projecting to conical, with or without an obvious shine. Frons usually narrow, occasionally wide, parallel or strongly diverging, usually without a prominent callus. Antennae flagellum with eight distinct flagellomeres, occasionally with distinct projections or fusion of the basal flagellomeres. Palpi sexually dimorphic, ranging from either small, rounded and flat, to large, slender and tapering or knife-like,

usually with a distinct lateral bare area, concavity or apical pit. Proboscis ranging from either short, less than the height of the head, and thick with well-developed labella, or long, greater than one and a quarter times to over twice the head length, with small, slender labella. Scutum with or without conspicuous vittae. Abdomen either small rotund to large or narrow parallel sided, with or without distinct markings or lateral fringes of hair. Wings either clear, smoky, spotted or strongly marbled; cell R_5 open, narrowed or closed petiolate; cell M_3 usually open, although often narrowed or closed in some genera; vein R_4 curved or angulate, with or without a short appendix. Hind tibial spurs always present, slender and moderate in length. Mackerras (1955, p. 482) described the genitalia as having the "style of male hypopygium single, usually finger-like, sometimes pointed [and hooked: Mackerras 1960). Anterior gonopophyses of female rounded or conical, approximated to one another, and only moderately chitonised".

Key to females of the genera and subgenera of the tribe Scionini

1. Face strongly bulging, projecting or conical; wings conspicuously smoky brown or grey (Figures 13-18)..... 2

Face truncate to moderately bulging; wings either clear, radially stained or with markings on crossveins (Figures 2-12)..... 12

2. Palpi long, equal to length of antennal flagellum, knife-like, extremely slender, tapered and flat; face shining; proboscis exceeding length of the head and thorax combined (Figures 17 & 18)..... 3

Palpi short, less than the length of the flagellum, broad or triangular; face without shine; proboscis one and a quarter time the length of the head, never exceeding length of thorax (Figures 13-16)..... 9

3. Antennal flagellum cylindrical, without projections or conspicuous tufts of hair; wing cell R_5 open or narrowed only, vein M_1 without inflexion (Figure 17)..... 4

Antennal flagellum with projections or tufts of conspicuous hairs; wing cell R_5 closed with obvious petiole, vein M_1 with inflexion (Figure 18)..... 7

4. Face covered in many conspicuous long hairs; scutum with obvious vittae; wings with cell R_5 broadly open. Brazil..... *Fidena* (*Neopangonia*) Lutz, 1909

Face without conspicuously long hairs; scutum without obvious vittae; wings with cell R_5 usually closed..... 5

5. Femora and tibiae covered in long, dense conspicuous hairs. Bolivia, Brazil and Peru..... *Fidena* (*Laphriomyia*) Lutz, 1911

Femora and tibiae hairs short and sparse, without such long hairs..... 6

6. Frons with a basal callus-like protuberance; palpi relatively thick and swollen with a deep lateral concavity; wings with cell R_5 long petiolate. Argentina..... *Fidena* (*Leptofidena*) Kröber, 1930

Frons without protuberance; palpi flat and tapered, with a flat, broad lateral bare area; wings with cell R_5 without a long petiole. Argentina, Brazil, Bolivia, Chile, Colombia, Costa Rica, Ecuador, Mexico, Panama, Paraguay, Peru, Suriname, Uruguay, and Venezuela..... *Fidena* (*Fidena*) Walker, 1850

7. Antennal flagellum without structural projections, first flagellomere with an enlarged and conspicuous dense tuft of hair. Bolivia, Brazil and Ecuador..... *Pityocera* (*Pseudelaphella*) Kröber, 1930

Antennal flagellum with obvious structural projections..... 8

8. Flagellomeres with long projections on both dorsal and ventral surfaces, decreasing in size towards the tip. Panama and Ecuador..... *Pityocera* (*Pityocera*) Giglio-Tos, 1896

Flagellomeres with long projections on the dorsal surface only. Brazil, French Guiana, Peru and Suriname..... *Pityocera* (*Elaphella*) Bezzi, 1913

9. Scutum with strong vittae, almost always exceeding transverse suture; frons wide; wing cells R_5 and M_3 closed (Figure 16). Argentina, Brazil, Bolivia, Colombia, Ecuador, Guatemala, Mexico, Panama, Peru and Venezuela..... *Scione* Walker, 1850

Scutum with at least indications of vittae, subtle, occasionally exceeding transverse suture; frons narrow; wing cells R_5 usually open and M_3 always open (Figures 13-15)..... 10

10. Frons parallel; proboscis thick; palpi broad, flat and slightly rounded at tip, not obviously tapering; legs stout, short and thick; thorax usually densely covered with hairs (Figure 13). Brazil and Chile..... *Lepmia* Fairchild, 1969 **stat.n.**

Frons strongly diverging; proboscis slender; palpi distinctly tapering at tip; legs relatively long and slender; thorax rarely covered with dense hairs (Figures 14 & 15)..... 11

11. Palpi slender and thick, with obvious deep excavated lateral bare area; labella not obviously wider than the proboscis shaft (Figure 15). Argentina, Brazil, and Chile..... *Pseudoscione* Lutz, 1918 **stat.n.**

Palpi broad, triangular and obviously flattened, without distinct lateral bare area; labella only slightly wider than the proboscis shaft (Figure 14). Chile..... *Parosca* Enderlein, 1922 **stat.n.**

12. Proboscis short, less than or equal to head length, thick, labella large and obvious; palpi long, equal to or greater than half the length of the proboscis shaft (Figures 2-4, 9-12)..... 13

Proboscis long, exceeding the length of the head, slender, labella small and subtle; palpi small, less than half the length of the proboscis shaft (Figures 5-8)..... 19

13. Frons strongly diverging ventrally near subcallus (Figures 2-4)..... 14

Frons more parallel, never strongly diverging near subcallus (Figures 9-12)..... 16

14. Antennal flagellomeres indistinct, superficially appearing as five with fusion of the basal four flagellomeres; palpi swollen and club-like, with a rather vague lateral bare area (Figure 4). Chile..... *Pseudomelpia* Enderlein, 1922 **stat.n.**

Antennal flagellum with eight distinct flagellomeres; palpi not as above; Australia or New Zealand (Figures 2 & 3)..... 15

15. Palpi subcylindrical, with reduced apical pits (Figure 2). Australia and New Zealand..... *Anzomyia* Lessard, 2012

Palpi slender and tapered to broad and flat, with distinct lateral bare areas, often rotated dorsally (Figure 3). New Zealand..... *Aotearomyia* Lessard, **gen.n.**

16. Abdomen oblong to slightly rectangular, dorso-ventraly compressed; wings usually darkened on at least the radial margin, sometimes evanescent (Figures 9 & 10)..... 17

Abdomen stout and rounded, sometimes narrowed posteriorly; wings either clear, lightly uniform grey to brown or spotted, rarely stained radially (Figures 11 & 12)..... 18

17. Wings obviously stained radially with black; stigma prominent; cell R_5 open; abdomen without prominent lateral fringes of hair tufts (Figure 9). Australia..... *Apocampta* Schiner, 1867 **stat.n.**

Wings greyish, without distinct markings; stigma inconspicuous; cell R_5 open, narrowed or closed; abdomen with prominent lateral fringes of hair tufts (Figure 10). Argentina, Bolivia, Chile and Peru..... *Osca* Walker, 1850 **stat.n.**

18. Large species (length 16-24 mm); cell R_5 closed, sometimes petiolate; cell M_3 narrowed or closed (Figure 11). Australia..... *Triclista* Enderlein, 1922 **stat.n.**

Small to moderately-sized species (length 10-15 mm); cell R_5 widely open or narrowed, rarely closed; cell M_3 open (Figure 12). Australia..... *Scaptia* Walker, 1850

19. Frons almost completely parallel and flat; proboscis relatively short, less than one and a quarter times the head length; palpi flat and rounded, with an extremely shallow almost flat lateral concavity; stigma prominent (Figures 7 & 8)..... 20

Frons distinctly diverging and raised at centre; proboscis long, equal to or greater than one and a half times the head length; palpi thick and tapered, with deep lateral concavity; stigma inconspicuous (Figures 5 & 6)..... 21

20. Small (length 8-11 mm) rotund species, blowfly-like in appearance; palpi flat and leaf-like, with moderately-sized bare area; usually metallic or semi-metallic in luster, sometimes shining; scutum and abdomen without distinct patterns; wings clear and without marbling (Figure 7). Australia..... *Myioscaptia* Mackerras, 1955 **stat.n.**

Medium-sized (length 9-14 mm) robust species; palpi usually thick and flattened with a large bare area; usually brownish-grey, nonmetallic and without shine; scutum and abdomen usually with prominent vittae or colour patterns; wings with distinct marbling at the center of cells (Figure 8). Australia..... *Plinthina* Walker, 1850 **stat.n.**

21. Abdomen elongated, narrow parallel-sided, wasp-like species; frons wide, often with a distinct callus-like protuberance; face shining; antennal pedicel relatively long, approximately three times the length of the scape; wings yellowish-brown, with a darker brown distal staining towards tip (Figure 6). Australia..... *Palimmecomyia* Taylor, 1917 **stat.n.**

Abdomen stout and ovular; frons narrow, only slightly raised at centre; face without shine; antennal pedicel short, approximately double the length of the scape; wings usually with one or more darker clouds on cross veins, sometimes less obvious (Figure 5). Australia..... *Copidapha* Enderlein, 1922 **stat.n.**

Genus *ANZOMYIA* Lessard, 2012

(Figure 2)

Anzomyia Lessard in Lessard & Yeates 2012a, p. 104. Type species *Scaptia* (*Pseudoscione*) *anomala* (Mackerras, 1960), Australia, by designation of Lessard & Yeates 2012a.

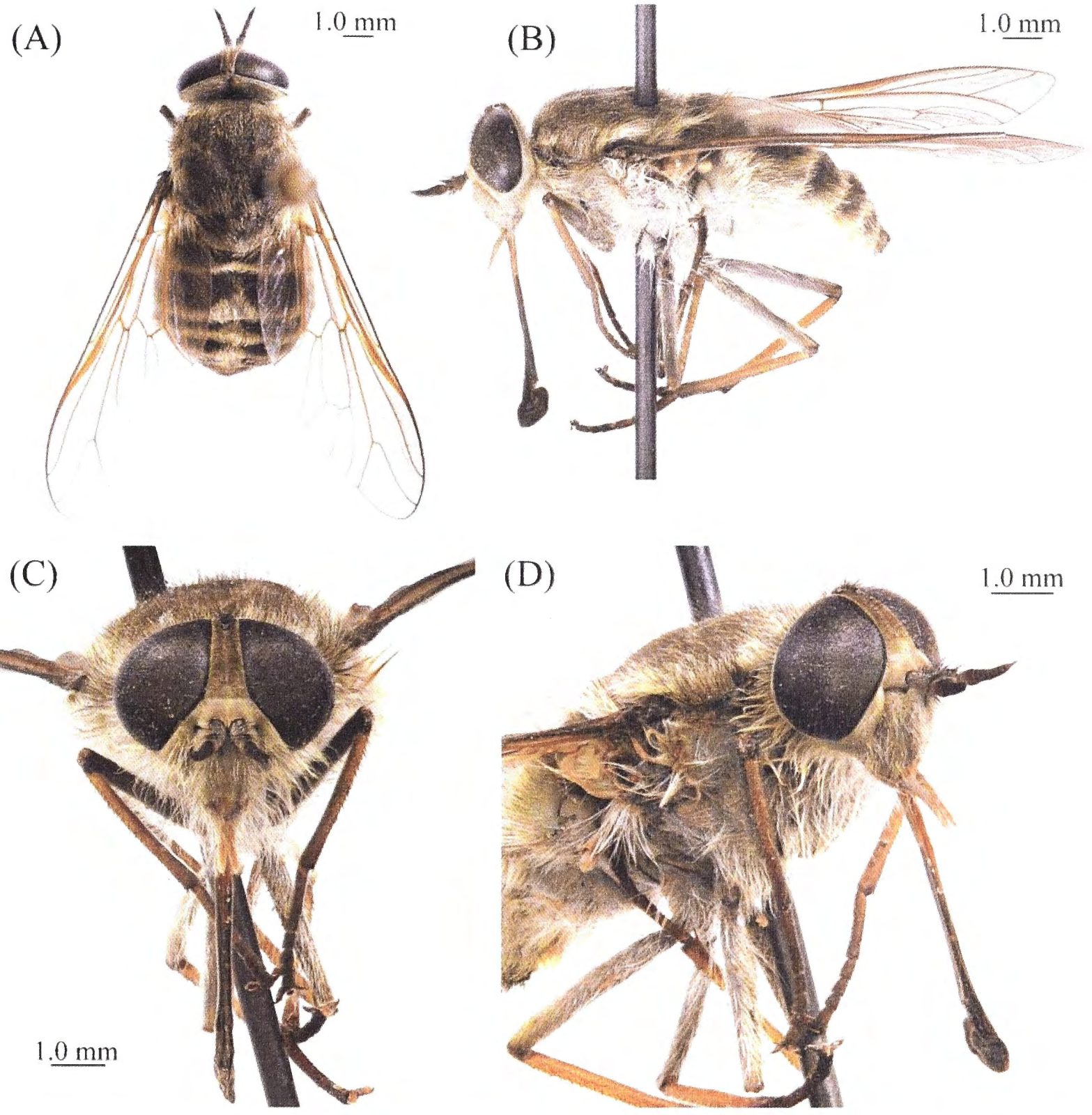

Figure 2: *Anzomyia* Lessard, 2012, female of type species *Scaptia* (*Pseudoscione*) *anomala* Mackerras, 1960: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

Type species. *Scaptia* (*Pseudoscione*) *anomala*, Mackerras, 1960 (Figure 2), Australia, by original designation of Lessard & Yeates (2012a, p. 104).

Morphological diagnosis. Small (length 6-10 mm), hairy and rather concolorous dark species (Figure 2), with a diverging frons, proboscis usually short and thick, and subcylindrical palpi. Distinguished from *Aotearomyia* Lessard, **gen.n.** by the smaller size and slender cylindrical palpi with reduced apical pits.

Female. Small (length 6-10 mm), dark and hairy species. Eyes hairy. Frons relatively narrow, strongly diverging (index 2.2 to 2.5), occasionally slightly raised at centre, with distinct subcallus. Face truncate to moderately bulging, or relatively projecting, without

shine. Antennae scape and pedicel small, flagellum mostly cylindrical, tapering at tip with eight distinct flagellomeres without projections. Palpi long, equal to length of flagellum, usually half the length of the proboscis shaft, very slender, subcylindrical and fusiform, with small apical pits reduced to flat ovals. Proboscis short, usually less than the length of the head, thick, with well-developed labella wider than the proboscis shaft. Scutum with at least indications of vittae, sometimes exceeding the transverse suture. Abdomen short and rotund to narrowed at tip, with indications of medial vittae. Wings usually brown or greyish, never marbled or spotted; stigma brown and inconspicuous; cell R_5 widely open; cell M_3 always open; R_4 angulate to slightly curved, without appendix (Lessard & Yeates 2012a). Genitalia originally described by Mackerras (1960, p. 120) as "small, with rounded gonophophyses, unchitonised 10th tergite, truncate cerci, lateral arms of the furca rather large, and caudal ends of the spermathecal ducts long, lightly chitonised".

Male. Similar to the female but hairier and somewhat darker. Eyes holoptic, with upper facets not obviously enlarged. Palpi shorter and more cylindrical than females (Lessard & Yeates 2012a). Mackerras (1960) stated that the genitalia are similar to the former subgenus *Scaptia* (*Pseudoscione*) without major structural modifications, with the style of the hypopygium finger-like and rounded at tip.

Species included. A valid key to all four known species (Species List) was provided by Lessard & Yeates (2012a).

Distribution. Australia and New Zealand. Occurring in high altitude mountainous regions of the Great Dividing Range in southeast Australia, ranging from New South Wales and the Australian Capital Territory to Victoria, in addition to the Southwest Alpine Fault in the South Island of New Zealand (Lessard & Yeates 2012a; Lessard *et al.* 2013; Mackerras 1960).

Biology. There is currently no information regarding the biology, feeding habits or larval stages for the genus.

Remarks. *Anzomyia* is accepted as a valid genus of the Scionini based on the distinct morphology and firm genetic divergence of the genus to all other Scionini (Figure 1). Moreover, *Anzomyia* and *Aotearomyia* Lessard, **gen.n.** are early offshoots of the Scionini

lineage based on the strong sister position to the remaining genera (Figure 1). The distinct phylogenetic position of the genus confirms Lessard and Yeates' (2012a) decision to establish *Anzomyia* as a unique genus of Scionini, rather than a subgenus of *Scaptia*. Although unnamed at the time, Mackerras hypothesised that *Anzomyia,* based on the intermediate anatomical form, may represent a unique derivation of the ancient Scionini lineage (Mackerras 1955), and was most likely the earliest form adapted to nectar feeding of early flowering plants (Mackerras 1960). The type species and the New Zealand species *An. herculensis* Lessard, 2012 are desired for future molecular and biogeographic studies.

Genus *AOTEAROMYIA* Lessard, gen.n.

(Figure 3)

Type species. *Pangonia adrel* Walker, 1850 (Figure 3), New Zealand, by present designation (ANIC).

Morphological diagnosis. Stoutly built and hairy flies (Figure 3), with a narrow and almost parallel frons that diverges only at the ventral margin, distinguished from *Anzomyia* by the large, slender and tapered palpi with a conspicuous lateral bare area that is often dorsally rotated.

Female. Length 8-12 mm. Eyes hairy. Frons extremely narrow (index usually 2.0 to 5.6), almost parallel, becoming moderately diverging at the basal quarter of frons, occasionally raised at centre. Face truncate to bulging, without shine. Antennal scape and pedicel relatively small, with the scape only slightly wider than the flagellum with eight distinct flagellomeres without projections. Palpi usually pointed and long, equal to the length of the flagellum and half the length of the proboscis shaft, occasionally broad and short, less than the length of flagellum, with a well-defined bare lateral area or concavity, often rotated dorsally. Proboscis short, usually equal to or less than the head length, thick, with large well-developed labella, wider than the proboscis shaft. Scutum with relatively prominent vittae, sometimes exceeding transverse suture. Abdomen broad and ovular, with medial tufts of hair. Wing suffused with brown along veins; stigma inconspicuous; cell R_5 open, narrowed or closed; cell M_3 open; vein M_1 without inflexion; R_4 curved or angulate, with or without a short appendix (Kröber 1931; Mackerras 1955, 1957, 1960). Mackerras (1957, p. 586) described the genitalia as having the "ninth tergite an undivided,

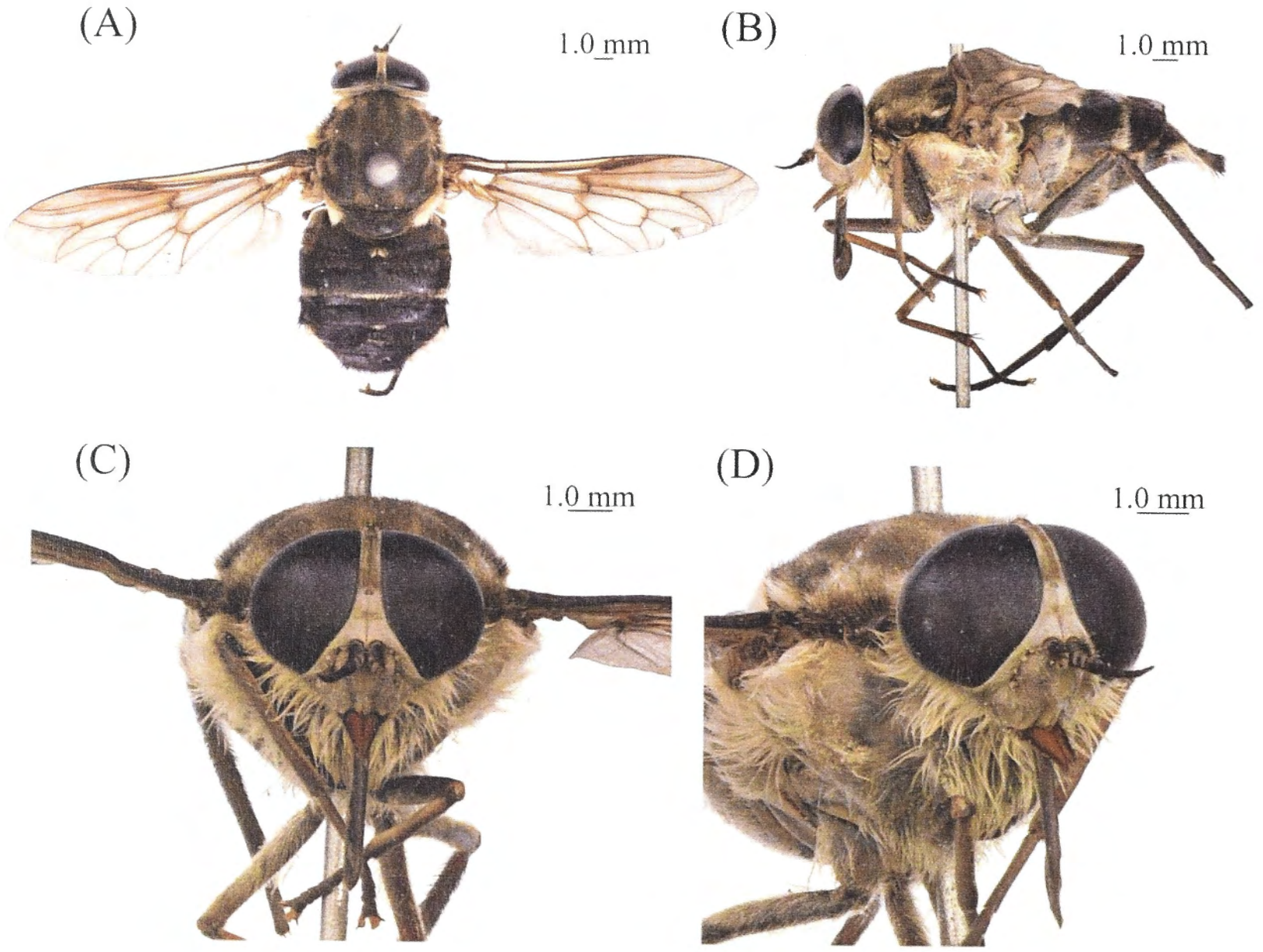

Figure 3: *Aotearomyia* Lessard, **gen.n.**, female of type species *Pangonia adrel* Walker, 1850: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

transverse bar; cerci obliquely truncate apically; caudal ends of spermathecal ducts lightly chitinised, without mushroom-like expansion".

Male. Length 8-14 mm. Darker and hairier than females. Eyes holoptic, with only slightly enlarged upper facets. Palpi short, slender and tapered, more pointed than females, occasionally rod-like, with a conspicuous lateral bare area (Mackerras 1955, 1957, 1960). Mackerras (1957, p. 586) described the genitalia as having the "ninth tergite large, undivided, forming a prominent shield over the other parts; aedeagus and coxites smooth; style simple, finger-like, rounded at tip".

Species included. A valid key to all six known species (Species List) was provided by Mackerras (1957).

Etymology. The name is derived from *Aotearoa,* the Māori name for New Zealand, combined with the Greek *myia*, meaning fly.

Distribution. New Zealand. Extensively dispersed along the alpine fault region of both the North and South Islands, ranging from the Northland to Southland regions (Lessard *et al.* 2013; Mackerras 1957).

Biology. Several species are known to feed abundantly on the flowers of *Leptospermum,* including *Aotearomyia adrel* (Walker, 1850), *Aotearomyia lerda* (Walker, 1850), and *Aotearomyia milleri* (Mackerras, 1957) (Lessard & Yeates 2012b; Mackerras 1957, 1960; Tillyard 1926). Blood-feeding is rarely witnessed, although *Ao. adrel* has been recorded to disturb cattle stocks (Mackerras 1957). Some species are quite social and often exhibit a form of dance where two individuals join their legs in flight and begin to spin rapidly in a tight circle (personal observation; Mackerras 1957). It is unknown whether this is an act of courtship between the males and females, or an exhibition of sexual competition among males vying for the attention of the female.

Larval habits are unknown for the genus, although one *Ao. adrel* male was bred from a larva and the pupal skin is preserved in the ANIC (Mackerras 1957, fig. 2A, p. 586). Mackerras (1957, p. 590-591) described the pupal aster as "remarkable, in that all six lobes are clearly represented, although the dorsal and ventral pairs are greatly reduced". He further hypothesised that it is the "most primitive" form of the limited Scionini larvae recorded, as those of *Copidapha, Myioscaptia* and *Scaptia* all possess "bilobed asters with the dorsal and ventral lobes reduced to low, unarmed swellings and the lateral lobes usually larger than in [*Ao.*] *adrel*".

Remarks. *Aotearomyia* Lessard **gen.n.** is hereby accepted as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation of the genus to all other Scionini (Figure 1). Moreover, *Aotearomyia* Lessard **gen.n.** is defined to include the New Zealand species *Ao. adrel*, *Aotearomyia brevipalpis* (Kröber, 1931), *Ao. lerda*, *Aotearomyia montana* (Hutton, 1901), *Aotearomyia milleri* and *Aotearomyia ricardoae* (Hutton, 1892), which have been transferred from their previous position within the former subgenus *Scaptia* (*Pseudoscione*), based on the shared morphology of the narrow and almost parallel frons and large, slender and tapered palpi. Mackerras (1957, p. 595) alluded to the monophyly of the New Zealand species stating "the whole group had a common ancestry, which had diverged somewhat from

the direct ancestry of the Australian species on the one side and the South American species on the other".

Genus *PSEUDOMELPIA* Enderlein, 1922 stat.n.

(Figure 4)

Pseudomelpia Enderlein, 1922, p. 343. Originally listed as monotypic for *Pseudomelpia horrens* Enderlein, 1925, Chile, in Enderlein's (1922, p. 343) taxonomic key to the tribe Silviini and officially described sometime later by Kröber (1930b, p. 138). Fairchild (1966a, p. 3).

Scaptia Walker, 1850, subgenus *Pseudomelpia* (Enderlein, 1922). First recognised as a subgenus of *Scaptia* by Mackerras (1955, p. 495, 1960, p. 4). Fairchild (1969, p. 203); Fairchild & Burger (1994, p. 38); Coscarón & González (2001, p. 31); Coscarón & Papavero (1993, pp. 18, 62, 2009, pp. 9, 56).

Type species. *Pseudomelpia horrens* Enderlein, 1925 (Figure 4), Chile, by original designation of Enderlein (1922, p. 343).

Morphological diagnosis. A small (length 7-9 mm), dark and hairy, monotypic genus (Figure 4), most similar to *Anzomyia,* but distinguished by the extremely short and thick proboscis, basal four antennal flagellomeres appearing as fused, and with short swollen club-like palpi.

Female. Length 7-9 mm. Eyes hairy. Head spherical and densely hairy. Eyes densely covered in long hairs. Frons relatively wide (index usually 2.0) and diverging, flat at centre. Face truncate and bulging, with only slight depression at the sides, without shine. Antennal scape somewhat swollen, pedicel normal, slightly thicker than the width of the flagellum, with eight indistinct flagellomeres, the basal four appearing as fused, making the flagellum superficially seem as being five segmented, without projections. Palpi long, equal to the length of flagellum and as long as the shaft of the proboscis, relatively flattened, blunt and significantly rounded at tip, somewhat swollen at base, appearing almost club-like, with a vague apical bare concavity. Proboscis extremely short, usually less than the head length, relatively thick and chitonised, with large and well-developed labella, wider than the proboscis shaft. Scutum with well-defined vittae exceeding the transverse suture. Abdomen short and rounded, with irregular black markings. Wings cloudy near cross veins; stigma inconspicuous; cell R_5 open; cell M_3 open; vein M_1 without inflexion; R_4 angulate, without appendix (Coscarón & Papavero 2009; Coscarón

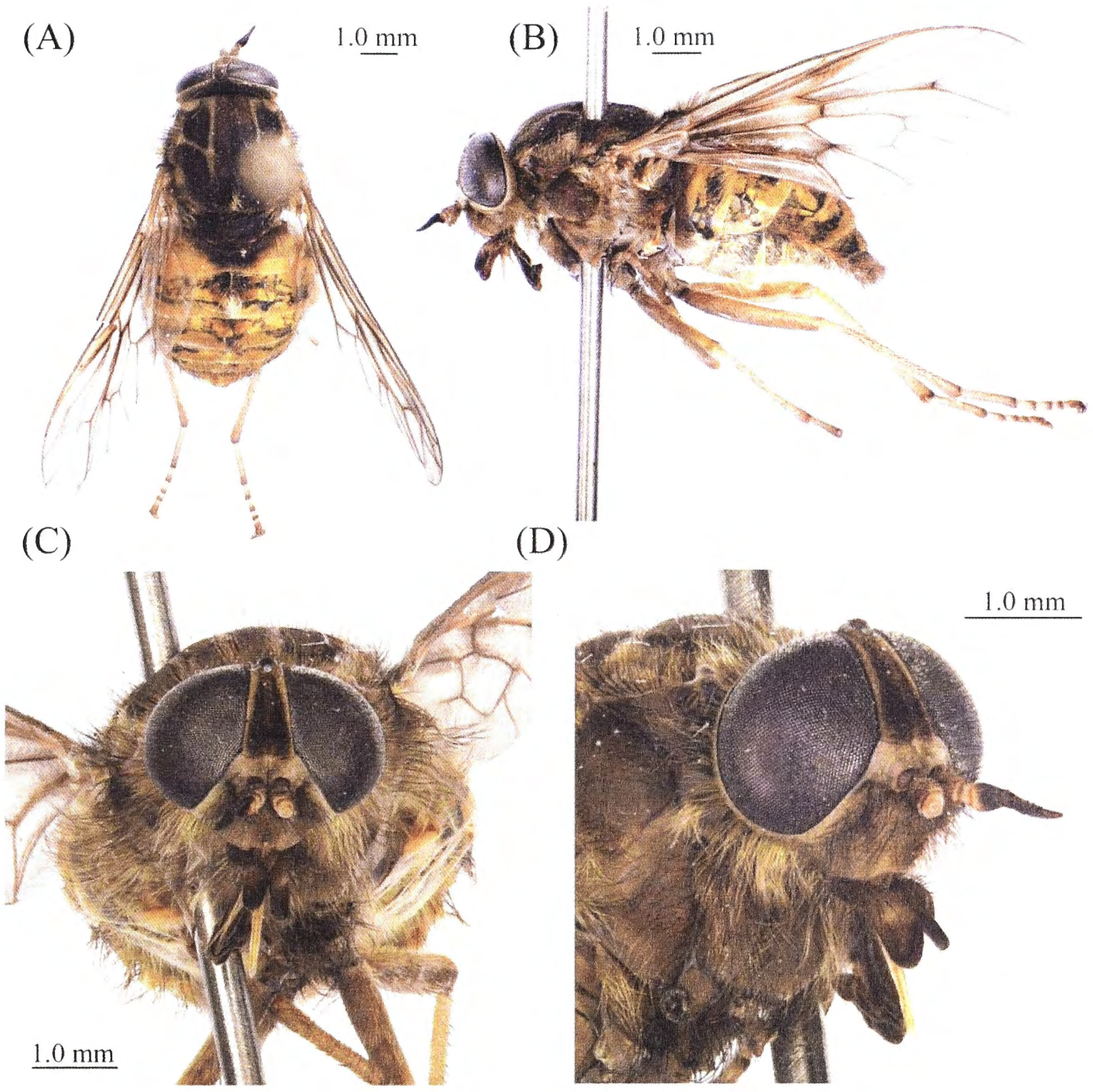

Figure 4: *Pseudomelpia* Enderlein, 1922 **stat.n.**, female of type species *Pseudomelpia horrens* Enderlein, 1925: (a) dorsum; (b) side; (c) frons; (d) profile (NMH).

& González 2001; Kröber 1930b; Mackerras 1955). Mackerras (1955, p. 495) described the genitalia as having the "eighth sternite of unusual shape, with very small, weak gonopophyses; genital fork large and conspicuous; 9th tergite strong, 10th weak; cerci apically rounded, only slightly flattened apically".

Male. Length 8-9 mm. Eyes holoptic, with upper facets enlarged. Palpi short, subcylindrical, slender and tapered, with long hairs and a reduced apical pit (Coscarón & González 2001; Mackerras 1955). Antennae as in female. Mackerras (1955, p. 496) described the genitalia as having the "style of hypopygium rounded; aedeagus strongly chitinised, and of rather unusual form".

Species included. The genus is represented by the type species only (Species List).

Distribution. South America. Southern Chile, ranging from the Talca to Aisén Provinces (Coscarón & González 2001).

Systematics. Although absent in the current molecular phylogenetic hypothesis for the tribe, *Pseudomelpia* is expected to be closely related to *Anzomyia* (Figure 1), based on the shared morphology of the short fleshy proboscis and large hairy antennal scape (Mackerras 1960; Lessard & Yeates 2012a).

Biology. According to Coscarón and González (2001), both sexes are entirely nectar feeding and do not exhibit any blood-feeding behaviours. Larval stages are unknown for the genus.

Remarks. *Pseudomelpia* is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology of the genus described above. Mackerras (1955, 1960) hypothesised that *Pseudomelpia,* along with the specimens that would eventually be described as *Anzomyia*, may represent an ancient derivation of the Scionini lineage that became early adapted to flower feeding. The genus is desired for future molecular analysis.

Genus *COPIDAPHA* Enderlein, 1922 stat.n.

(Figure 5)

Clanis Walker, 1850, p. 9, misapplied name of Hübner (1816; Lepidoptera). Type species *Pangonia contigua* Walker, 1848 (= *Pangonia lasiophthalma* Macquart, 1834), Australia, by designation of Coquillett (1910, p. 524).

Copidapha Enderlein, 1922, p. 337, 1925, p. 270. Originally listed as monotypic for *Copidapha bifasciata* Enderlein, 1925 (= *Pangonia roei* Macleay, 1826), Australia, in Enderlein's (1922, p. 337) key to the former subfamily Melpiinae and officially described sometime after by Enderlein (1925, p. 230). Reduced to synonym of *Scaptia* by Ferguson (1926, p. 303). Snonomysed as *Scaptia* (*Pseudoscione*) Lutz in Lutz, Araujo, and Fonseca, 1918 by Mackerras (1955, p. 493) who indicated it would remain available if the Australian members needed distinction from the remaining *Scaptia* (*Pseudoscione*) species. Mackerras (1955, p. 493, 1960, p. 81, 1964, p. 79), Daniels (1989) and Lessard & Yeates (2012b) continued to treat *Copidapha* as a synonymy of *Scaptia* (*Pseudoscione*).

Lilaea Enderlein, 1922, p. 341, 1925, p. 297, misapplied name of Walker, 1850, by wrong selection of *Pangonia roei* Enderlein, 1922, which was actually the misapplied name of Macleay, 1826 (= *Pangonia concolor* Walker, 1850), Australia as type species (Mackerras 1960). Corrected by Ferguson (1926, pp. 294, 304).

Scaptiella Enderlein, 1923, p. 544. Monotypic for *Pangonia aperta* Loew, 1859, "Lusitania", (= *Pangonia subappendiculata* Macquart, 1850), Australia.

Astypia Enderlein, 1925, p. 297. Type species *Pangonia jacksonii* Enderlein, 1925, misapplied name of Macquart, 1838 (= *Scaptia* (*Pseudoscione*) *calabyi* Mackerras, 1960), Western Australia, by original description.

Type species. *Pangonia roei* Macleay, 1826 (Figure 5), Australia, by original designation of Enderlein (1922, p. 337; under synonym *Copidapha bifasciata* Enderlein, 1925).

Morphological diagnosis. Mostly medium to rather large (range 9-16 mm) plump species (Figure 5), with a moderately diverging frons, long slender proboscis with small labella, and relatively long slender legs. Distinguished from *Pseudoscione* by the truncate to moderately bulging face, wide palpi, and labella only slightly wider than the proboscis shaft.

Female. Length 9-17 mm. Eyes hairy, sometimes extremely short and sparse as in the type species. Frons relatively narrow and strongly diverging (index usually 1.9 to 4.0), slightly raised at centre. Face less protuberant, truncate to moderately bulging, without obvious shine. Antennal scape and pedicel small, width equal to the cylindrical and tapered flagellum, with eight distinct flagellomeres without projections. Palpi long, equal to length of the flagellum, sometimes relatively short, less than length of the flagellum, always one-third the length of the proboscis shaft, usually think, pointed, occasionally truncate or slender, and with a well-defined lateral bare concavity that is either wide or narrow. Proboscis long and slender, ranging between one and a half times to twice the length of the head, with a small, moderately developed labella usually only slightly wider than the proboscis shaft. Scutum with or without conspicuous vittae. Abdomen ovular, either rounded or narrowed at end, with or without prominent markings. Wings usually with at least a darker cloud across apices of basal cells, or with a prominent second band at fork of R_{4+5}; stigma inconspicuous; cell R_5 often narrowed or closed; cell M_3 always open; vein M_1 without inflexion; vein R_4 angulate, usually without appendix (Enderlein 1925; Mackerras 1955, 1957, 1960 figs 41, pp. 124-147). Mackerras (1960, p. 83) described the genitalia as having the "eighth sternite with gonopophyses usually

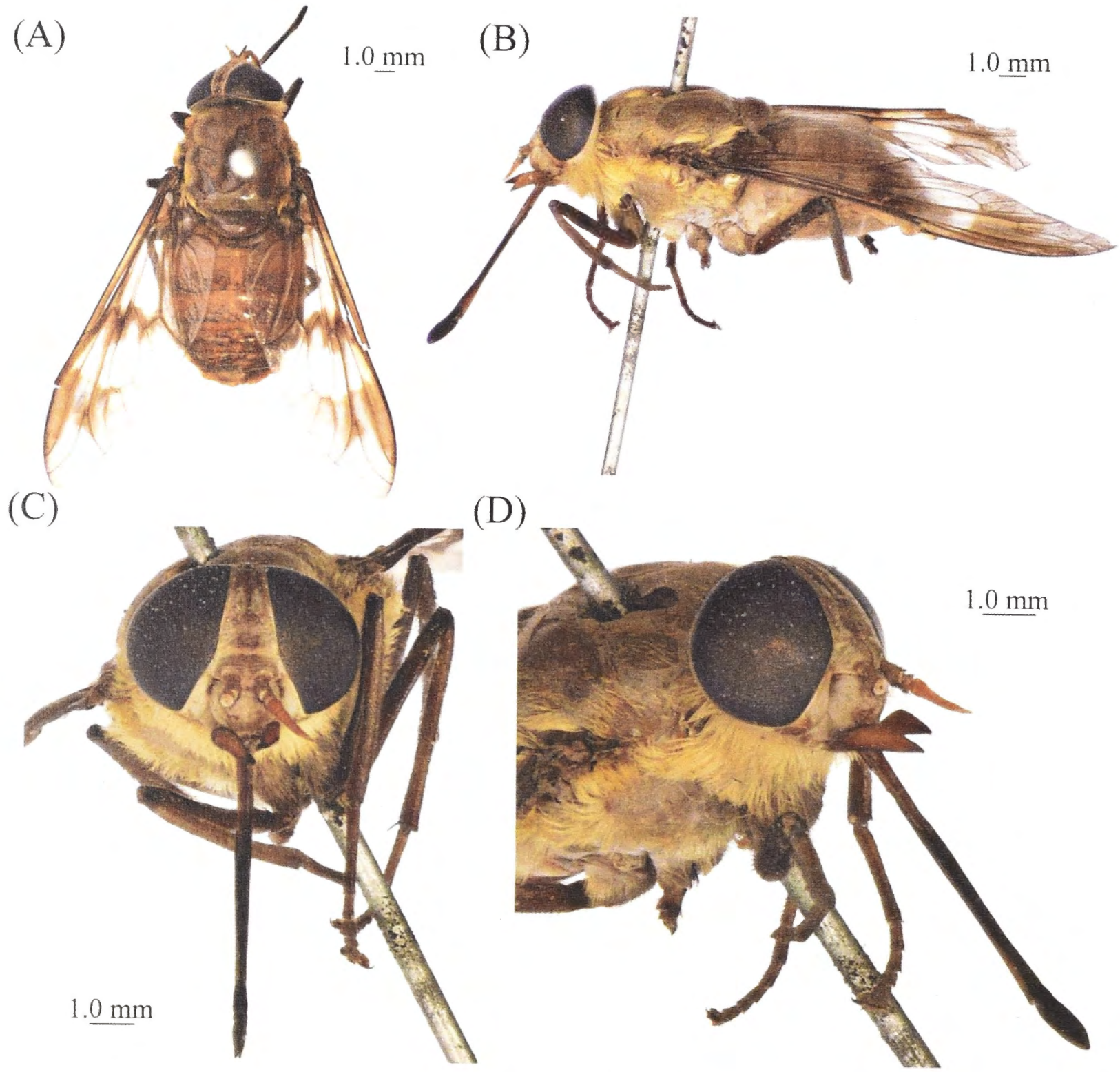

Figure 5: *Copidapha* Enderlein, 1922 **stat.n.**, female of type species *Pangonia roei* Macleay, 1826: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

triangular and approximated apically; cerci often truncate apically; lateral arms of furca not fused with 9th tergite".

Male. Length 9-15 mm. Eyes holoptic, with upper facets slightly enlarged. Palpi stout and cylindrical, somewhat tapering at tip, in some cases only slightly longer than the females, with a small, subapical, lateral bare area. Style of hypopygium finger-like and rounded towards the tip (Mackerras 1960, fig. 41).

Species included. An updated key to all 32 known Australian species was provided by Lessard and Yeates (2012b), whereas Mackerras (1964) provided a valid key to the eleven known species from New Guinea (Species List).

Distribution. Australia and New Guinea. Mainly a coastal Australian fauna, ranging from tropical northern Queensland to southern Victoria, with smaller populations in south-central South Australia and south-west Western Australia (Lessard & Yeates 2012b, fig. 2; Mackerras 1960, fig. 20). There are also two isolated species each from central Australia and Tasmania. The New Guinea species are restricted to the high mountainous regions of the island (Mackerras 1964; Oldroyd 1947).

Biology. The genus is both nectar and blood-feeding, with adult females of *Copidapha georgii* (Taylor, 1918), *Copidapha gemina* (Walker, 1848), *Copidapha regisgeorgii* (Taylor, 1918), *Copidapha xanthopilis* (Ferguson, 1921), *Copidapha concolor* (Walker, 1850), and *Copidapha neoconcolor* (Mackerras, 1960) recorded to feed on humans, with the latter two also known to attack horses (Lee *et al.* 1957; Lessard & Yeates 2012b; Mackerras 1960; personal communication). The species *Copidapha subappendiculata* (Macquart, 1850) and *Copidapha quadrimaculata* (Walker, 1848) are known to attack cattle (Ferguson & Henry 1920). Many adults feed on the nectar of the tea-tree genus *Leptospermum,* including *Copidapha calabyi* (Mackerras, 1960) and *Copidapha vicina* (Taylor, 1918) which were also recorded to feed from *Eucalyptus* (Lessard & Yeates 2012b; Mackerras 1960). Interestingly some species such as *Copidapha maculiventris* (Westwood, 1835) and *Copidapha subcontigua* (Ferguson, 1921) have a varied diet of horses, humans and *Leptospermum* (Mackerras 1960). The feeding habits of the New Guinean species have not been recorded.

Only two larvae have been found and described for the Australian species *C. vicina* collected from the soil and among decaying leaves and grass (English 1955). Larvae appear to be wider and slightly longer than those of *Scaptia* and *Myioscaptia*, and possess a distinct lateral fringe of long bristles on the aster, compared to the shorter and more spine-like fringe of the latter two genera (Mackerras 1960, figs 7-18, p. 9).

Remarks. *Copidapha* is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation to all other genera of the Scionini (Figure 1). Moreover, the recent molecular results of Lessard *et al.* (2013) confirmed Lessard and Yeates' (2012b) decision to formally raise *Copidapha guttipennis* (Ferguson, 1924) and *Copidapha occidentalis* (Mackerras, 1960) from subspecies to species level, as each formed a distinct and well-supported monophyletic clade in the previous phylogenetic analysis.

Regarding the geographical divisions of the genus, the New Guinean species are considered to be northern radiations of the morphologically analogous Australian *maculiventris* subgroup (Mackerras 1961, 1964). Moreover, there are two isolated Australian species unplaced within *Copidapha*, including *Copidapha mackerrasi* (Lessard, 2012) and *Copidapha ianthina* (White, 1915). *Copidapha mackerrasi* is the only known member of the genus to occur in central Australia, over 900 km inland from the nearest coastline, and has such distinct morphology that it may represent a putative new genus of Scionini (Lessard & Yeates 2012b). *Copidapha ianthina* is the only species of the genus to occur in Tasmania and represented by a single specimen only. It is also more similar to the New Zealand species *Ao. adrel* than any other Australian species based on the shared morphology of the almost parallel frons and slender palpi (Mackerras 1960). Therefore more extensive sampling of *C. mackerrasi, C. ianthina* and New Guinean species is warranted for future molecular studies.

Genus *PALIMMECOMYIA* Taylor, 1917 stat.n.

(Figure 6)

Palimmecomyia Taylor, 1917b, p. 518. Originally monotypic for *Palimmecomyia celaenospila* Taylor, 1917 (= *Pangonia walkeri* Newman, 1857), Queensland, Australia, by original designation. Ferguson (1926, p. 300).

Scaptia Walker 1850, subgenus *Palimmecomyia* (Taylor, 1917). Mackerras (1955, p. 498, 1960, p. 142); Daniels (1989).

Type species. *Pangonia walkeri* Newman, 1857 (Figure 6), Australia, by original designation of Taylor (1917, p. 518; under synonym *Palimmecomyia celaenospila* Taylor, 1917).

Morphological diagnosis. Long (13-17 mm), narrow, elongated and parallel-sided wasp-like species (Figure 6), most similar to *Copidapha*, but distinguished by the peculiar shining wax-like cuticle, orange wings with striking brown staining at tips, and abdomen with distinct brown markings at the medial and lateral margins.

Female. Length 13-17 mm. Eyes hairy. Frons wide (index usually 2.0 to 2.4), slightly diverging, sometimes raised at centre to form a rudimentary callus. Face truncate to

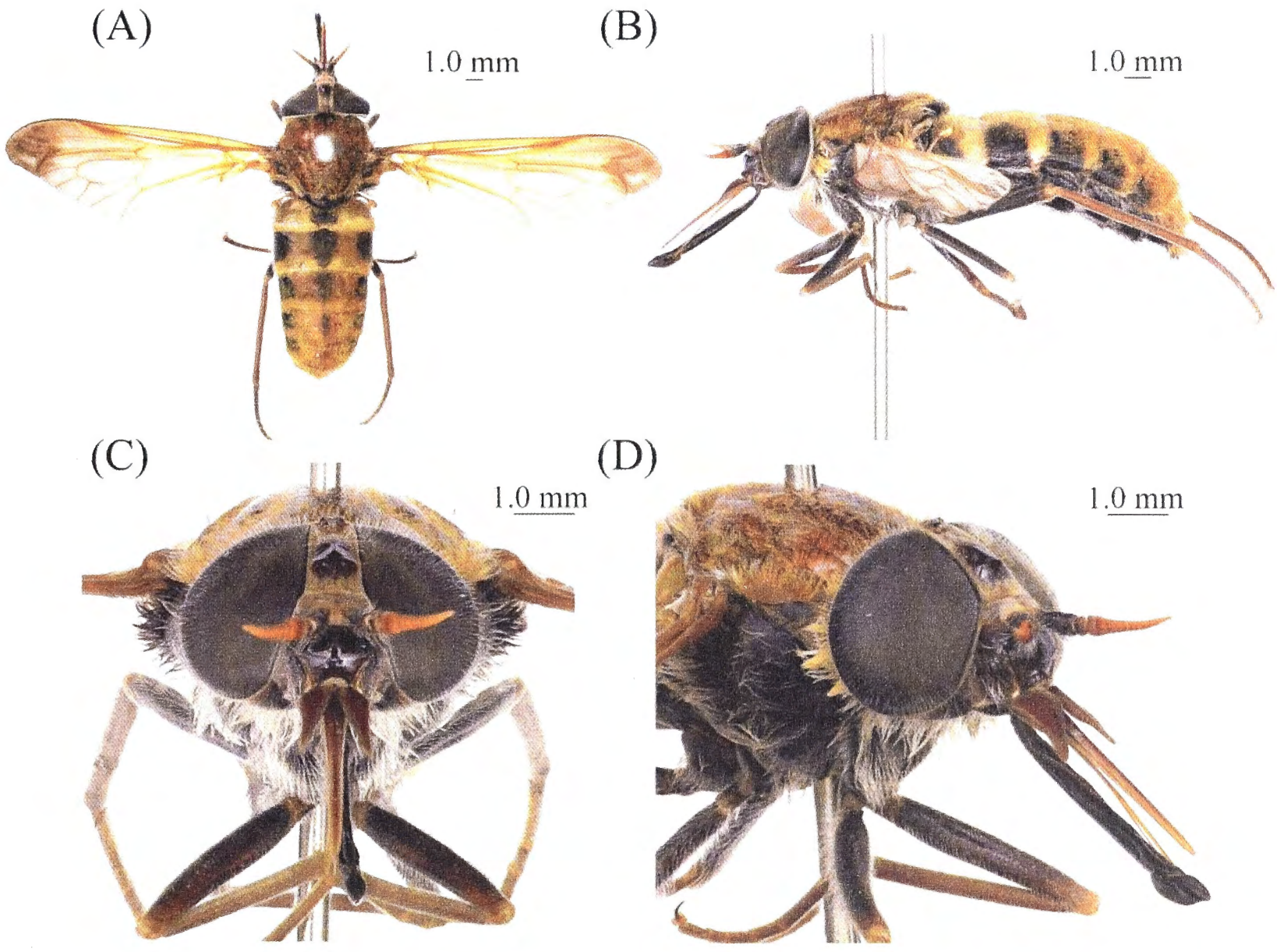

Figure 6: *Palimmecomyia* Taylor, 1917 **stat.n.**, female of type species *Pangonia walkeri* Newman, 1857: (a) dorsum; (b) side; (c) frons; (d) profile (AM).

bulging, with depressions at base and sides, distinctly shining. Antennal scape relatively long, almost half the length of the flagellum, pedicel small, both equal to width of flagellum with eight distinct flagellomeres without projections. Palpi relatively long, equal to length of the flagellum and slightly less than half the length of the proboscis shaft, thick and pointed with a well-defined lateral bare concavity. Proboscis relatively long, approximately one and a half times the length of the head, slender and chitonised, with relatively small but moderately developed labella, only slightly wider than the proboscis shaft. Scutum with at least indications of vittae. Abdomen long, length at least twice the width, and narrow parallel-sided, marked with dark brown patches at the medial and lateral margins. Wings orange to brown, with dark brown infuscated tips; stigma inconspicuous; cell R_5 usually closed, sometimes open; cell M_3 open; vein M_1 without inflexion; R_4 angulate, with or without a small appendix (Ferguson 1926; Taylor 1917; Mackerras 1960). Mackerras (1960, p. 142) described the genitalia as having the "eighth sternite with gonopophyses subtriangular; cerci rounded apically; lateral arms of furca fused with 9th tergite".

Male. Length 13-16 mm. Eyes holoptic, with upper facets enlarged. Palpi short, slender, cylindrical, obliquely truncate at tip, and with a distinct lateral bare area. Mackerras (1960, p. 142) described the genitalia as having the "ninth tergite deeply incised distally; aedeagus and coxite normal; style hooked and pointed at tip, but not unusually wise, nor with zone of conspicuous hairs".

Species included. A valid key to the only two known species (Species List) was provided by Mackerras (1960, p. 142).

Distribution. Australia. Predominantly occurring in the eastern coast of southern Queensland and northern New South Wales (Mackerras 1960, fig. 22). There also appear to be two aberrant and isolated populations in Western Australia and South Australia (Mackerras 1960) (see Remarks).

Systematics. Although absent in the current molecular phylogenetic hypothesis for the tribe, morphological evidence suggests that *Palimmecomyia* is closest related to *Copidapha* (Figure 1), both sharing the diverging frons, the relatively long and slender proboscis with less developed labella, and small, thick and pointed palpi that have an obvious lateral bare concavity.

Biology. Nothing is known regarding the feeding and larval habits for the genus.

Remarks. *Palimmecomyia* is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology described above. The genus is extremely rare, with limited material available for examination. Only a handful of specimens have been collected for both species over the last hundred years, and consequently, the collection records for the genus are extremely poor; for the few specimens collected for *Palimmecomyia pictipennis* Mackerras, 1960, records merely read "S. Australia" and "Darling Range", with the latter presumably from Western Australia. Mackerras (1960, p. 145) stated "neither record can be accepted unreservedly until more specimens are discovered". Therefore, more extensive material, including the type species, is desired for future morphological and molecular analyses.

Genus *MYIOSCAPTIA* Mackerras, 1955 stat.n.

(Figure 7)

Scaptia Walker 1850, subgenus *Myioscaptia* Mackerras, 1955a (fig. 30, p. 496). Type species *Pangonia violacea* Macquart, 1850, Australia, by original designation. Fairchild & Mackerras (1977); Mackerras (1955, p. 496, 1960, p. 122); Daniels (1989, 2011); Lessard & Yeates (2013).

Type species. *Pangonia violacea* Macquart, 1850 (Figure 7), Australia, by original designation of Mackerras (1955, p. 496).

Morphological diagnosis. Small (8-11 mm) and rotund species (Figure 7), often appearing to mimic blowflies, either brightly colourful and metallic or dull and semi-metallic in lustre, most similar to *Plinthina* but separated by the smaller size, short rounded and leaf-like palpi, and less obvious scutal vittae and abdominal markings.

Female. Length 8-11 mm. Eyes hairy. Frons usually parallel, sometimes only slightly diverging dorsally and ventrally, narrow (index usually 2.5 to 4.3), slightly raised at centre. Face truncate to moderately bulging, with depressions at base and sides, rarely shining. Antennae scape and pedicel small, equal to width of stout cylindrical flagellum with eight distinct flagellomeres without projections. Palpi short, usually less than the length of flagellum and less than one third the length of the proboscis shaft, flattened, broad and leaf-like, with a well-defined flat bare area. Proboscis relatively small, less than one and a quarter times the head length, relatively slender, heavily chitonised, usually with well-developed labella usually wider than the proboscis shaft. Scutum either metallic or non-metallic, sometimes shining, usually without conspicuous vittae that rarely exceeds the transverse suture. Abdomen short and rotund, either metallic or non-metallic, sometimes shining, without obvious markings. Wings clear; stigma prominent; cell R_5 narrowed, or closed with a short petiole; cell M_3 open; vein M_1 without inflexion; R_4 angulate, with or without appendix (Mackerras 1955, 1960). Mackerras (1960, p. 122) described the genitalia as having the "eight sternite with gonopophyses rounded; cerci rounded apically; lateral arms of furca relatively large, narrowly fused with lateral edge of 9th tergite".

Male. Length 8-10 mm. Eyes holoptic, with upper facets slightly enlarged. Palpi short, slender, cylindrical and blunt, with an obvious apical lateral bare area. Mackerras (1960, p. 122) described the genitalia as having the "hypopygium with aedeagus unusually long;

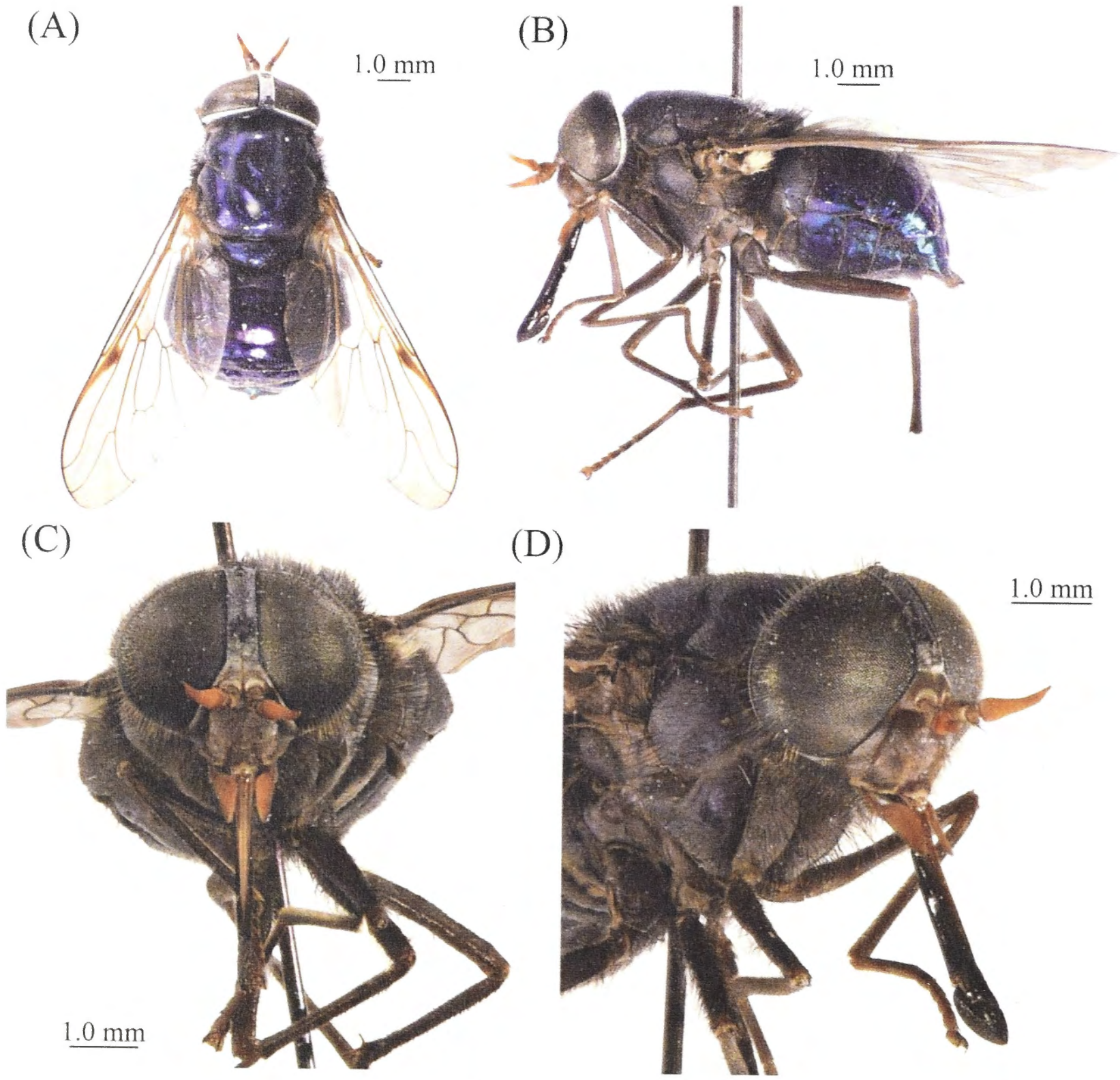

Figure 7: *Myioscaptia* Mackerras, 1955 **stat.n.**, female of type species *Pangonia violacea* Macquart, 1850: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

coxites normal; style hooked and pointed at tip, but not unusually wide, and without strong hairs".

Species included. An updated key to all eleven known species (Species List) was provided by Lessard & Yeates 2013.

Distribution. Australia. Predominantly a temperate eastern coast genus, ranging from tropical north Queensland to southern Victoria. There is also a smaller Western Australian radiation corresponding to *Myioscaptia lambkinae* Lessard, 2013 and *Myioscaptia gibulla* (Walker, 1848), both recorded 270 km inland from the coast in dry and drought

prone environments (Lessard & Yeates 2013, fig. 1; Lessard *et al.* 2013; Mackerras 1960, fig. 21).

Biology. *Myioscaptia* is largely blood-feeding, with *Myioscaptia calliphora* Mackerras, 1960, *Myioscaptia ferromontana* Daniels, 2011 *Myioscaptia inopinata* Fairchild & Mackerras, 1977, *M. violacea* and *Myioscaptia bancrofti* (Austen, 1912) all recorded to feed on humans, with the latter two also known to attack cattle (Fairchild & Mackerras 1977; Daniels 2011; Mackerras 1960). Most species exhibit the unusual behaviour of mimicking the general appearance of blowflies, including the sound and general low level approach to flight (Nicholson 1927; Mackerras 1955, 1960).

The larval and pupal stages have been described for only one species, *Myioscaptia muscula* (English, 1955), with the larvae found developing in sandy cave floors and the ledges of sandstone cliffs, sometimes coexisting with ant lion larvae (English 1955; Mackerras 1955, 1960). Of the limited number of Scionini larvae found, they appear to be shorter and more slender than the *Copidapha* larvae (Mackerras 1960, figs 7-18, p. 9), and have short and more spine-like lateral tufts on the aster, most similar to *Scaptia* larvae.

Remarks. *Myioscaptia* is hereby raised to genus level and is recognised as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation from the remainder of the Scionini (Figure 1).

Genus *PLINTHINA* Walker, 1850 stat.n.

(Figure 8)

Plinthina Walker, 1850, p. 10. Originally monotypic for *Pangonia macroporum* Macquart, 1838 (= *Pangonia binotata* Latreille, 1812), Australia, by original designation. Ferguson (1924, p. 253, 1926, p. 299); Mackerras (1955, p. 497).

Scaptia Walker 1850, subgenus *Plinthina* (Walker, 1850). First recognised as a subgenus of *Scaptia* by Ferguson (1926, p. 299). Mackerras (1955, 1960); Daniels (1989); Lessard & Yeates (2011, p. 242).

Type species. *Pangonia binotata* Latreille, 1812 (Figure 8), Australia, by original designation of Walker (1850, p. 10; under synonym *Pangonia macroporum* Macquart, 1838).

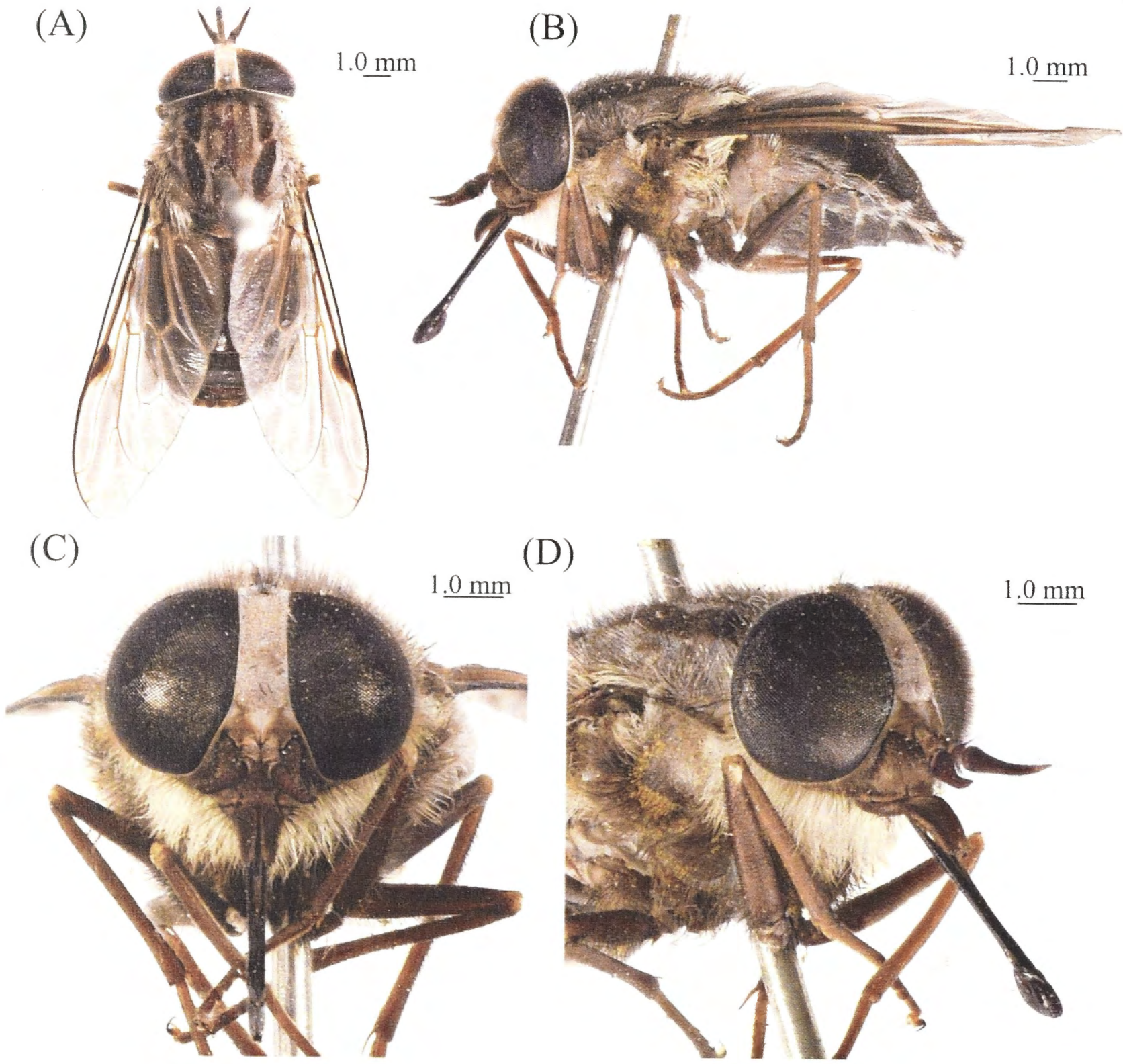

Figure 8: *Plinthina* Walker, 1850 **stat.n.**, female of type species *Pangonia binotata* Latreille, 1812: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

Morphological diagnosis. Medium-sized (9-14 mm) species, most similar to *Myioscaptia* but distinguished by the distinct marbling of the wings, although sometimes rather subtle, short thick and broad flattened palpi, with prominent scutal vittae and usually with distinct markings on the abdomen (Figure 8).

Female. Length 9-14 mm. Eyes hairy. Frons narrow, usually parallel, sometimes slightly diverging (index usually 2.7 to 3.8), rarely raised at centre. Face truncate to slightly bulging, rarely shining. Antennal scape and pedicel small, equal to width of the tapering flagellum with eight distinct flagellomeres without projections. Palpi usually relatively short, less than the length of flagellum and always less than a quarter of the length of the proboscis shaft, usually thick, rounded apically, flattened, with a well-defined lateral bare

area. Proboscis relatively short, less than one and a quarter times the head length, moderately slender, chitonised, with relatively small, moderately developed labella usually as wide as the proboscis shaft. Scutum usually with conspicuous vittae exceeding transverse suture, sometimes less defined. Abdomen rotund to ovular, occasionally with distinct banding or patterns. Wing usually distinctly marbled with conspicuous brown staining in the cells, sometimes evanescent or clear; stigma prominent, usually brown; cell R_5 closed, often with a long petiole; cell M_3 open; vein M_1 without inflexion; R_4 angulate, with or without an appendix (Lessard & Yeates 2011; Mackerras 1960). Mackerras (1960, p. 131) described the genitalia as having the "eighth sternite often unusually wide, fused with lateral edge of 9th tergite. The two halves of the 10th tergite also tend to fuse with each other and with the 9th, evidently a further expression of a need for rigidity in these parts".

Male. Length 9-11 mm. Eyes holoptic, with upper facets enlarged. Palpi short, slender, cylindrical, blunt at tip, and with a lateral bare area distally. Mackerras (1960, p. 131) described the genitalia as having the "hypopygium with aedeagus long; coxite thick and often rigid; style wide, strongly hooked and pointed at tip, and with a zone of conspicuous, short, thick hairs about middle".

Species included. An updated key to all twelve known species (Species List) was provided by Lessard and Yeates (2011).

Distribution. Australia. Predominantly dispersed along the eastern coast ranging from north Queensland to northern New South Wales, with three smaller radiations in southeastern Western Australia, the northern coast of Western Australia and the northeast coast of the Northern Territory (Lessard & Yeates 2011, fig. 1; Lessard *et al.* 2013; Mackerras 1960, fig. 22).

Biology. The genus is largely blood-feeding, with *Plinthina clelandi* (Ferguson, 1921), *Plinthina divisa* (Walker, 1850), *Plinthina vertebrata* (Bigot, 1892) and *Pl. binotata* recorded to feed on cattle (Mackerras 1960), with the latter also a "vicious and persistent biter" of humans (Mackerras 1960, p. 7). Larval habits are unknown for the genus.

Remarks. *Plinthina* is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation to the

remainder of Scionini (Figure 1). Based on previous collection records, the genus appears to be well adapted to tolerate arid environments, particularly *Plinthina arnhemensis* Lessard, 2011 and *Pl. clelandi,* which have been collected 180 km and 280 km inland from the nearest coastline, respectively. The aridification of central Australia may have been a driving force for the speciation of the genus. Moreover, Mackerras (1955) suggested that the genus evolved in Western Australia and radiated eastwards. Conversely, the current molecular phylogenetic hypothesis for the Scionini (Lessard *et al.* 2013) suggest that *Plinthina* may have originated in the eastern coast and later radiated to the Northern Territory and Western Australia, as the Queensland species recovered as sister to the remainder of Northern Territory and Western Australian species.

Genus *APOCAMPTA* Schiner, 1867 stat.n.

(Figure 9)

Apocampta Schiner, 1867, p. 310, 1868, p. 96. Monotypic for *Apocampta nigra* Schiner, 1868 (= *Chrysops subcana* Walker, 1848), Australia, by designation of Schiner (1868). Enderlein (1922, p. 336, 1925, p. 268). Reduced to a synonym of *Scaptia* by Ferguson (1926, p. 300). Daniels (1989); Mackerras (1960, p. 37 fig. 53, p. 50, p. 51 fig. 82).

Type species. Monotypic for *Chrysops subcana* Walker, 1848 (Figure 9), Australia, by designation of Schiner (1867, 1868; under synonym *Apocampta nigra* Schiner, 1868).

Morphological diagnosis. A small (length 9-12 mm) slender, concolorous black, shining monotypic genus (Figure 9), with a narrow oblong abdomen, differentiated from *Ocsa* by the smaller size, abdomen without obvious lateral fringes of hair, and wings infuscated with dark brown to black radial staining.

Female. Length 9-12 mm. Eyes hairy. Frons relatively narrow, nearly completely parallel and only slightly diverging at base (index 1.7), mostly flat at centre. Face truncate to slightly bulging, with basal indentation and depression at sides, without shine. Antennae with short scape and pedicel, flagellum relatively cylindrical, tapering, with eight distinct flagellomeres without projections. Proboscis relatively short and thick, approximately equal to the length of the head, with large, well-developed labella wider than the proboscis shaft. Palpi long, equal to or greater than the length of the flagellum, only slightly shorter than half the length of the proboscis, narrow, slender and sabre-like, with a flat well-

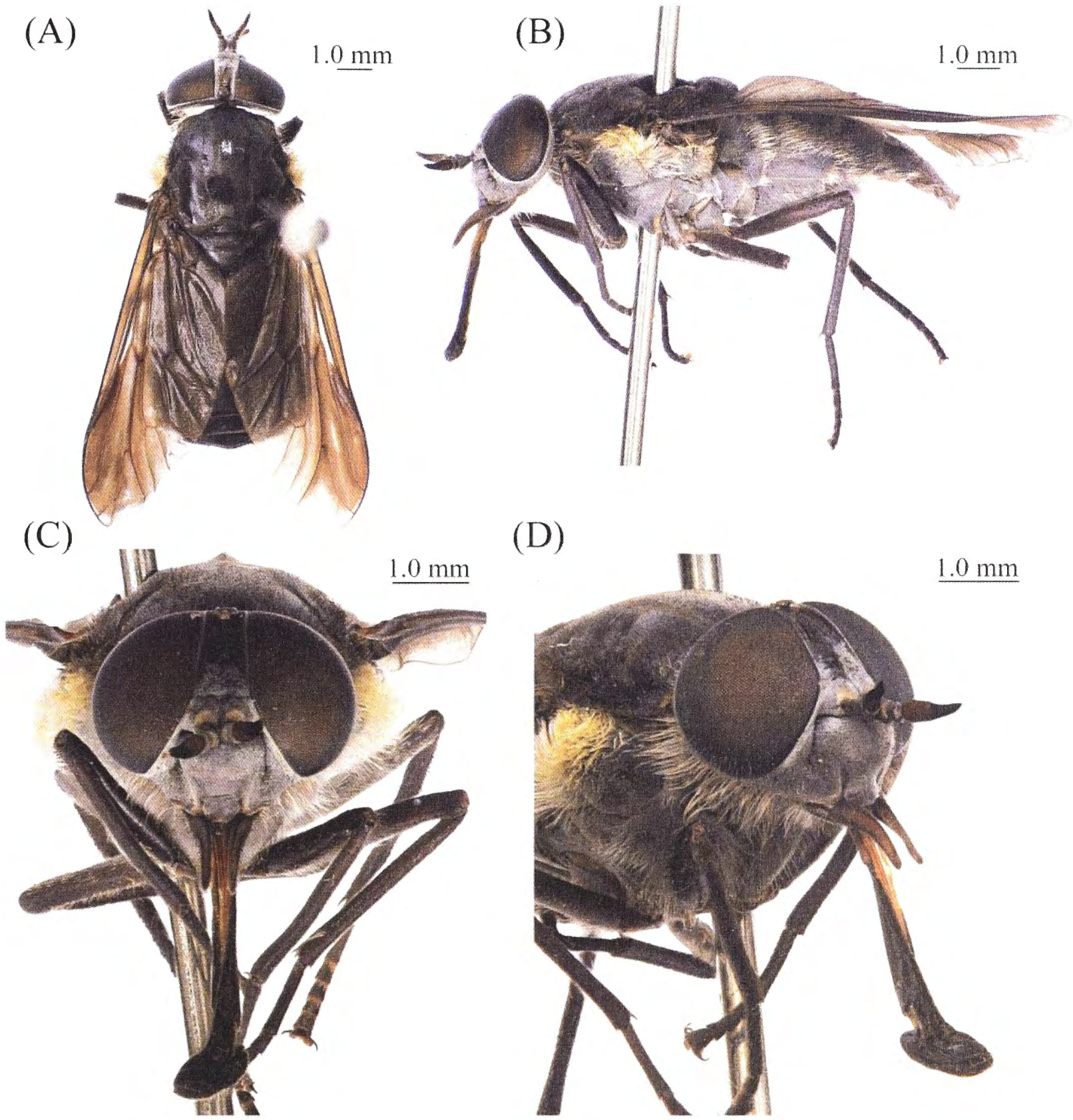

Figure 9: *Apocampta* Schiner, 1867 **stat.n.**, female of type species *Chrysops subcana* Walker, 1848: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

defined lateral bare area or concavity. Scutum with at least traces of vittae. Abdomen slender, elongated oblong to elliptical in shape, without obvious marginal fringes of hair. Wings infuscated brown to black, darkest along radial area; stigma prominent, dark brown to black; cell R_5 open; cell M_3 widely open; vein M_1 without inflexion; R_4 curved without appendix (Enderlein 1925; Mackerras 1960; Schiner 1868). Genitalia with eighth sternite gonophyses rounded, apically truncated cerci, with the lateral arms of furca without being fused to the 9th tergite (Mackerras 1960).

Male. Length 9-11 mm. Hairier and thicker than females. Eyes holoptic, with upper facets only slightly enlarged. Palpi slender, subcylindrical, slightly tapered, with a reduced

lateral bare area. Genitalia with a finger-like style of the hypopygium that is somewhat rounded at the tip (Mackerras 1960).

Species included. The genus is represented by the type species only (Species List).

Distribution. Australia. Dispersed along the eastern coast, ranging from northern Queensland to southeastern New South Wales and the Australian Capital Territory (Lessard *et al.* 2013; Mackerras 1960).

Biology. The genus is recorded to feed on the blood of humans (Mackerras 1960). Larval stages are unknown for the genus.

Remarks. *Apocampta* is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology and strong genetic divergence from all remaining Scionini (Figure 1).

Genus *OSCA* Walker, 1850 stat.n.

(Figure 10)

Osca Walker, 1850, p. 10. Type *Pangonia depressa* Macquart, 1837 (= *Tabanus latus* [= *lata*] Guèrin-Méneville, 1835), Chile, by designation of Coquillett (1910). Reduced to a synonym of *Scaptia* by Ferguson (1924, p. 256; 1926, p. 298), although Kröber (1930b, 1932, 1934) and others continued to use *Osca* for South American species. Mackerras (1955) did not morphologically separate *Osca* from *Scaptia* (*Scaptia*), but acknowledged that they did form a unique group of species. The following authors continued to treat *Osca* as a synonymy of *Scaptia*: Cárdenas *et al.* (2009); Chainey *et al.* (1994, p. 326); Coscarón & Papavero (1993, pp. 18, 61, 2009, pp. 9, 53); Coscarón & Wilkerson (1985, p. 277); Fairchild (1956, p. 9; 1966b, p. 354); Mackerras (1955, p. 490, 1960, p. 36); Philip (1967, p. 112); Wilkerson (1984, p. 434); Wilkerson & Fairchild (1984, p. 45).

Diatomineura Rondani, 1863. Type *Pangonia depressa* Macquart, 1837 (= *Tabanus latus* Guèrin, 1832), Chile, by designation of Coquillett (1910).

Bombomimetes Enderlein, 1922. Monotypic for *Pangonia rufoaurea* Philippi, 1865 (= *Pangonia rufa* Macquart, 1838), Chile. Synonymy by Kröber (1930b), with Mackerras (1955) agreeing upon examination of both sexes.

Calliosca Enderlein, 1925. Monotypic for *Calliosca schoenemanni* Enderlein, 1925 (= *Diabasis varia* Walker, 1848), Chile. Mackerras (1955) found nothing in the description or notes on the female to separate this genus from *Scaptia*. Fairchild (1956, p. 9; 1966a, p. 1) confirmed synonymy.

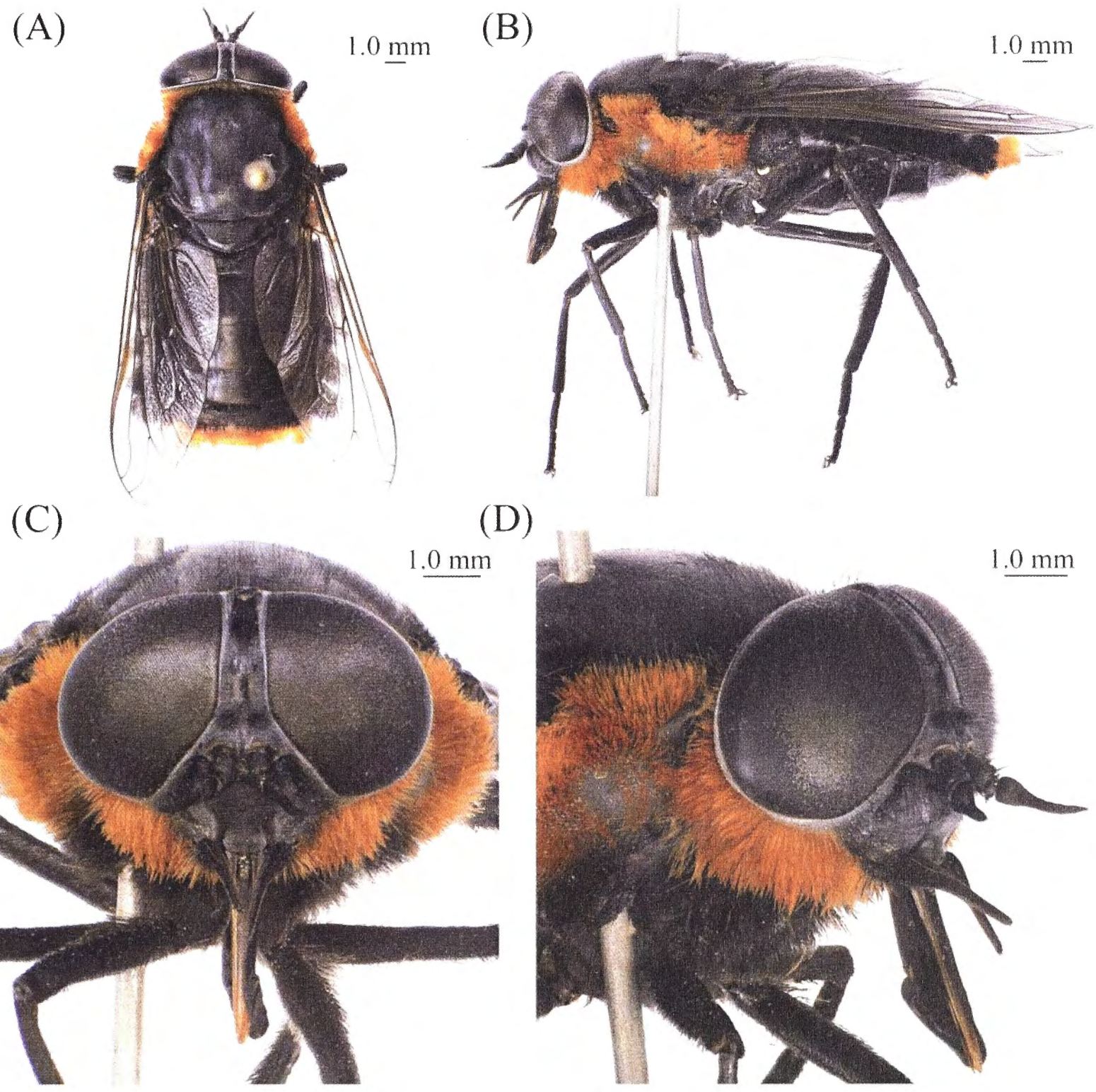

Figure 10: *Osca* Walker, 1850 **stat.n.**, female of type species *Tabanus lata* Guèrin-Méneville, 1835: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

Type species. *Tabanus latus* Guèrin-Méneville, 1835 (= *lata*; Figure 10), Chile, by designation of Coquillett (1910).

Morphological diagnosis. Moderately-sized (length 11-19 mm) and broadly built species (Figure 10), somewhat resembling bumblebees, with long thick legs and a rather broad oblong abdomen, separated from *Apocampta* by the less adorned wings and distinct dorsoventrally compressed abdomen with dense lateral fringes of hair.

Female. Length 11-19 mm. Eyes hairy. Frons very narrow (index usually 2.8 to 4.8), typically parallel, occasionally diverging either dorsally or ventrally, slightly raised narrowly at centre, subcallus slightly bulging but not distinctly separated. Face truncate

to somewhat bulging dorsally, with depressions at base and sides, at least partially shining. Antennal scape and pedicel small, equal to width of the flagellum, with eight distinct flagellomeres, the first three flagellomeres thick but not wider than the scape, and the distal flagellomeres narrowly tapering, without projections. Palpi long, exceeding length of the flagellum and at least half or equal to the length of the proboscis shaft, usually elongated, pointed and sabre-like, sometimes flattened, with a flat and well-defined lateral bare area or concavity. Proboscis very short, usually less than the length of the head, extremely thick and heavily chitonised, with large, well-developed labella usually wider than the proboscis shaft. Scutum with at least indications of vittae. Abdomen usually rather oblong and dorsoventrally compressed, with a dense lateral fringe of conspicuous hairs. Wings usually clear to greyish; stigma present, usually inconspicuous; cell R_5 usually open, sometimes narrowed or closed and petiolate; cell M_3 open; vein M_1 without inflexion; R_4 curved, with or without appendix. Genitalia with eight sternite width usually exceeding height, gonopophyses rounded at boarder, cerci usually indirectly truncated at the tip, occasionally subtrapezoidal, genital fork slightly convex, with slightly chitonised spermathecae (Coscarón & Papavero 2009; Coscarón & Wilkerson 1985; Kröber 1930b).

Male. Length 14.5-17 mm. Eyes holoptic, with upper facets slightly enlarged. Palpi shorter than female, subcylindrical, slightly tapered, with relatively broad and flat apical bare area. Genitalia with the gonocoxite width exceeding the length of the gonostylus, occasionally reversed with the gonostylus being longer than the basal width of the gonocoxite, gonostylus distally pointed, with an elongated epandrium, sometimes with two small median posterior lobes, and subtrapezoidal cerci (Coscarón & Wilkerson 1985).

Species included. A valid key to the majority of species (Species List) was provided by Coscarón and Wilkerson (1985), with one later described species *O. nigribella* (Wilkerson, 1984) identified in couplet nine (Wilkerson 1984).

Distribution. South America. Distributed in the temperate and high altitude regions of the Andeas, ranging from Bolivia and Peru to Argentina and Chile (Coscarón & Wilkerson 1985; Coscarón & Papavero 2009; Łessard *et al.* 2013).

Biology. The genus is blood-feeding in behaviour, with *O. lata* referred to as "an avid biter of humans and animals" (Coscarón & Wilkerson 1985, p. 289). Some members are expected to feed on the nectar of plants, as the abdomen of *O. lata* is occasionally full of nectar and quite sweet (pers. exp.).

Larvae and pupae of *O. lata* have been found developing within close proximity to decomposing tree trunks and in the roots of grass (Coscarón & González 1989). Larvae superficially appear to resemble the general shape, width and coloration patterns of *Myioscaptia* larvae, but differ in the aster possessing shorter and stouter horns, with thick lateral spines, more similar to *Scaptia* larvae. Coscarón and González (1989) agreed with English (1955) in that it can take up to two to three years for the larvae to complete development.

Remarks. *Osca* is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology and firm genetic separation from all remaining Scionini (Figure 1). Moreover, *Osca* is defined to include the eleven species presented in Table One. More species are required for future molecular sampling to confirm the monophyly of the genus, as the current molecular phylogenetic hypothesis for the Scionini includes only the type species *O. lata* (Lessard *et al.* 2013).

Genus *TRICLISTA* Enderlein, 1922 stat.n.

(Figure 11)

Erephopsis Rondani, 1863, p. 85. Enderlein (1925, p. 296) wrongly cited *Tabanus guttatus* (= *guttata*) Donovan, 1805 as type species.

Triclista Enderlein, 1922, p. 339. Originally listed as monotypic for *Pangonia limbinevris* Enderlein, 1922, Australia (= *Pangonia singularis* Macquart, 1846), in Enderlein's (1922, p. 338) key to the Scionini and officially described sometime after by Enderlein (1925, p. 304). Reduced to a synonym of *Scaptia* by Ferguson (1926, p. 299), adopted by Daniels (1989) and Mackerras (1955, p. 491, 1960, pp. 41-46).

Type species. *Pangonia singularis* Macquart, 1846 (Figure 11), Australia, by designation of Enderlein (1922, p. 339; under synonym *Pangonia limbinevris* Macquart, 1855).

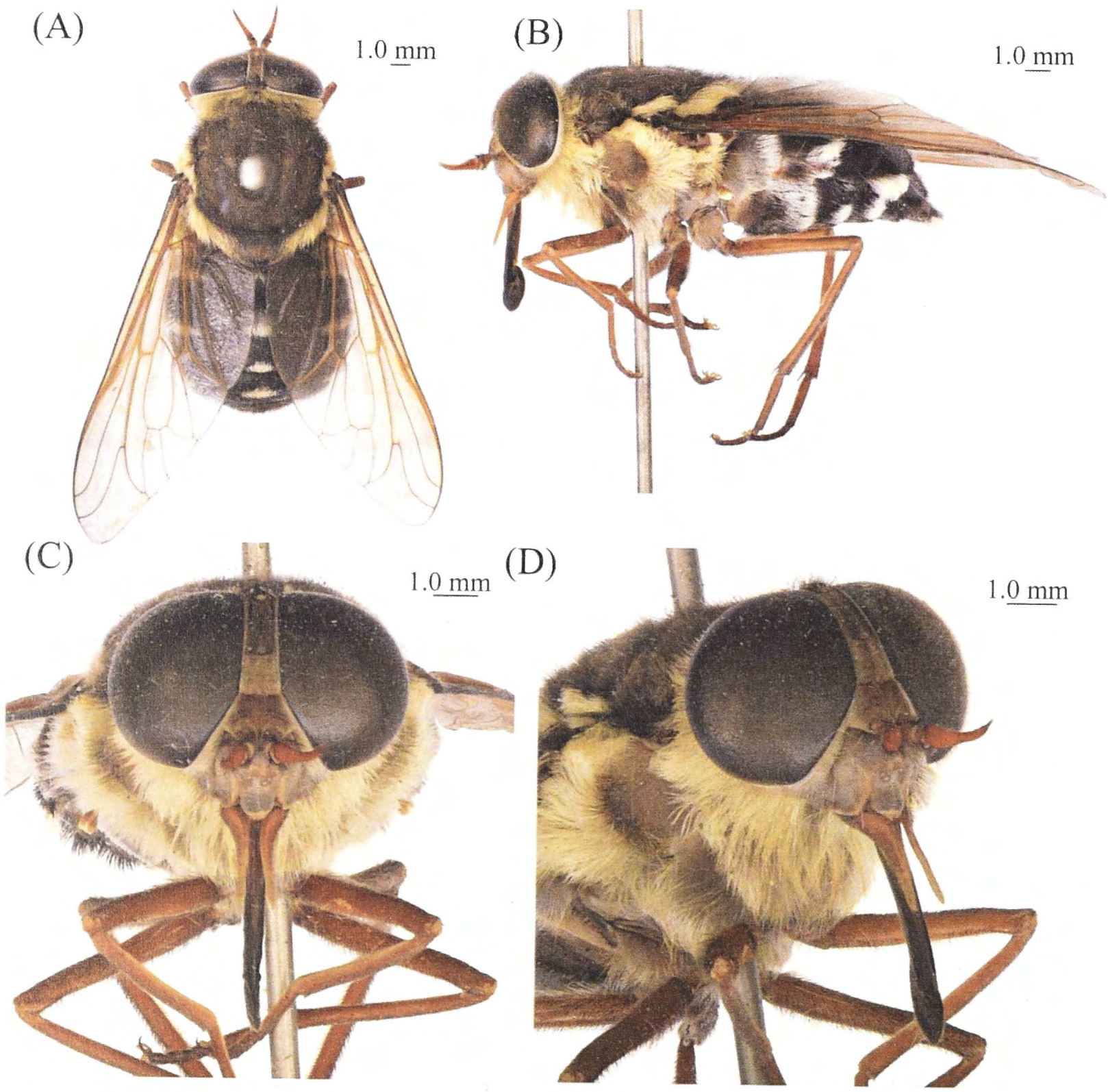

Figure 11: *Triclista* Enderlein, 1922 **stat.n.**, female of type species *Pangonia singularis* Macquart, 1846: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

Morphological diagnosis. Very large (16-24 mm) and robust species (Figure 11), with a short thick proboscis, long and rather sabre-like palpi, superficially similar to *Scaptia* but distinguished by the larger size, clouded wings usually with cells R_5 closed and M_3 closed or narrowed, and abdomen with obvious white patches.

Female. Length 16-24 mm. Eyes hairy. Frons narrow (index usually 3.0 to 4.3) and parallel, only slightly diverging or converging either dorsally or ventrally, slightly raised at centre, subcallus slightly bulging and distinctly separated. Face truncate, depressed at base and sides, without obvious shine. Antennal with short scape and pedicel, equal to basal width of tapering flagellum, with eight distinct flagellomeres without projections. Palpi long, exceeding length of the flagellum and longer than half the length of the

proboscis shaft, slender, pointed and sabre-like, with a well-defined bare lateral area. Proboscis small, equal to the length of the head, thick and heavily chitonised, with large, well-developed labella, wider than the proboscis shaft. Scutum with at least indications of scutal vittae, sometimes obvious and exceeding the transverse suture. Abdomen large and rotund, with distinct white medial patches. Wings clouded grey to smoky, usually with darker patches at basal crossveins; stigma inconspicuous; R_5 usually closed with petiole; cell M_3 usually narrowed, but occasionally closed and petiolate; vein M_1 without inflexion; R_4 angulate with or without appendix (Enderlein 1925; Mackerras 1960). Genitalia with eighth sternite gonopophyses rounded, cerci apically truncated and with lateral arms of the furca without being fused to the 9th tergite (Mackerras 1960).

Male. Length 11-18 mm. Eyes holoptic, usually with upper facets distinctly enlarged. Palpi small, cylindrical at base, apical half slender, occasionally broad, rather flat and slightly tapered at tip, with a moderate-sized flat bare area. Genitalia with style of hypopygium elongated, finger-like and rounded at tip (Mackerras 1960).

Species included. A valid key to all three known species (Species List) was provided in couplets 2-3 of Mackerras (1960, p. 39) key to the former subgenus *Scaptia* (*Scaptia*).

Distribution. Australia. Eastern coast ranging from southeastern Queensland to southern Victoria, with an isolated population in southwest Western Australia (Lessard *et al.* 2013; Mackerras 1960).

Biology. The genus is blood-feeding in behaviour, with *Triclista gutatta* (Donovan, 1805) and *T. singularis* recorded to attack humans, horses and livestock (Ferguson & Henry 1920; Mackerras 1960). *Triclista singularis* has been collected from *Eucalyptus* (personal observation) and is presumed to be nectar-feeding. Larval stages are unknown for the genus.

Remarks. *Triclista* is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation from all remaining Scionini (Figure 1).

Chapter Eight

Genus *SCAPTIA* Walker, 1850

(Figure 12)

Scaptia Walker, 1850, p. 8. Type species *Pangonia aurata* Macquart, 1838, Australia, by designation of Coquillett (1910, p. 603). Ferguson (1924, 1926).

Scaptia Walker, 1850, subgenus *Scaptia* Mackerras 1955, p. 490. Fairchild (1969, p. 203); Daniels (1989); Mackerras (1960, p. 36); Lessard & Yeates (2013).

Type species. *Pangonia aurata* Macquart, 1838 (Figure 12), Australia, by designation of Coquillett (1910, p. 603).

Morphological diagnosis. Mostly small to medium-sized (7-18 mm) solidly built species, with relatively short and strong legs (Figure 12), distinguished from other genera by the parallel frons, large pointed sabre-like palpi, short thick proboscis with large and well-developed labella, rather stout and rotund abdomen that is not obviously dorsoventrally compressed and wings with cells R_5 and M_3 open.

Female. Length 7-18 mm. Eyes hairy. Frons narrow, usually parallel or slightly converging ventrally (index usually 2.0 to 4.0), slightly raised at centre in some species, subcallus occasionally bulging and distinct. Face truncate, with depressions at the base and sides, without obvious shine. Antennal scape and pedicel small, almost equal to length of the flagellum, with eight distinct flagellomeres, widest on first basal segment and tapering at tip, without projections. Palpi long, usually equal to or greater than the length of the flagellum or greater than half the length of the proboscis shaft, sometimes only shorter than the flagellum length or half the length of the proboscis shaft, usually laterally compressed, pointed and sabre-like, and with a conspicuously broad lateral bare area. Proboscis short, usually as long as the head length, thick and heavily chitonised with large and well-developed labella wider than the proboscis shaft. Scutum with or without conspicuous vittae, occasionally exceeding transverse suture. Abdomen usually stout and rotund, either with or without obvious markings or patterns. Wing usually clear, occasionally spotted at crossveins or with radial suffusion; stigma often inconspicuous; cell R_5 usually open, sometimes narrowed, rarely closed; cell M_3 open; vein M_1 without inflexion; R_4 angulate, with or without appendix (Mackerras 1955, 1960). Mackerras (1960, p. 36) described the genitalia as having the "eighth sternite with gonopohyses often rounded; cerci often truncate apically; lateral arms of furca not fused with 9th tergite".

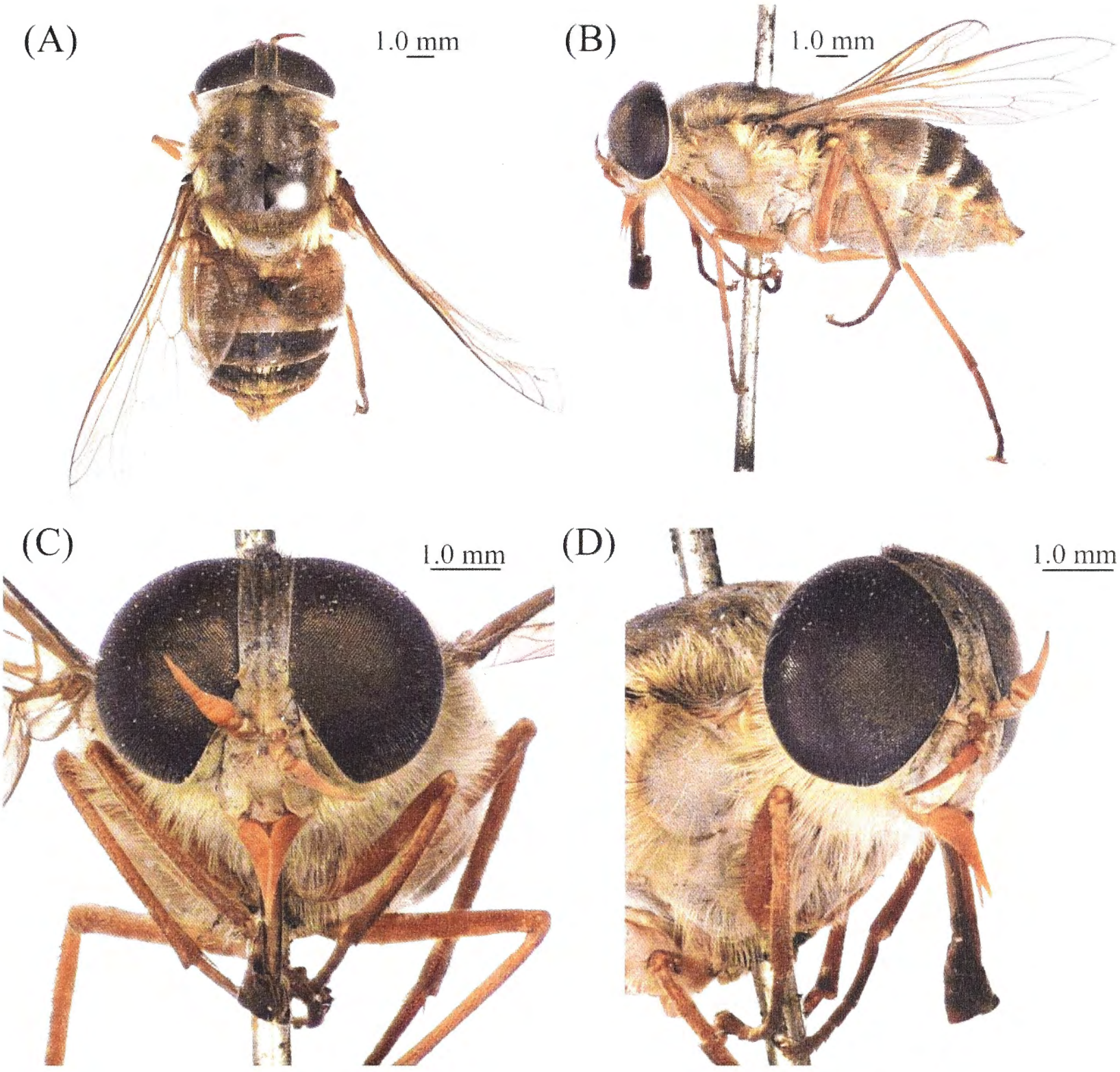

Figure 12: *Scaptia* Walker, 1850, female of type species *Pangonia aurata* Macquart, 1838: (a) dorsum; (b) side; (c) frons; (d) profile (NHM).

Male. Length 7-15 mm. Eyes holoptic, with upper facets only slightly enlarged. Palpi short and slender, cylindrical, blunt at tip, and with an apical lateral bare area. Mackerras (1960, p. 36) described the genitalia as having the "style of hypopygium finger-like, rounded at tip".

Species included. A valid key to species (Species List) was provided by Mackerras' (1960, p. 39) key to the former subgenus *Scaptia* (*Scaptia*), with the recently described species *S. aurinigra* Lessard, 2013 identified in couplet 11 (Lessard & Yeates 2013).

Distribution. Australia. Predominantly coastal, ranging from northern Queensland to southern Victoria, with three isolated populations in southern South Australia, southwest Western Australia, and Tasmania (Lessard *et al.* 2013; Mackerras 1960, fig. 19).

Biology. The genus is both nectar and blood-feeding, with *Scaptia brevirostris* (Macquart, 1850), *Scaptia pulchra* (Ricardo, 1915), *Scaptia similis* Mackerras, 1960 and *Scaptia testacea* (Macquart, 1838) recorded to bite humans (Mackerras 1960), and *Scaptia fulgida* (Ferguson & Henry, 1920) and *Scaptia monticola* Mackerras, 1960 collected from *Leptospermum* (Mackerras 1960; personal observation). The three species *Scaptia auriflua* (Donovan, 1805), *Scaptia jacksoniensis* (Guérin, 1831) and *Scaptia jacksonii* (Macquart, 1838) have all been observed to feed from both humans and flowers of *Leptospermum* (Lee *et al.* 1957; Mackerras 1960; White 1915).

Larvae and pupae have only been described for *Scaptia patula* (Walker, 1848). Larvae were collected from the surface of damp soil and among grass roots in the mountainous regions of southern New South Wales, and were found feeding on Tipulidae larvae (Fuller 1936; Mackerras 1955, 1960). Mackerras (1960, p. 10) described the larvae as "elongate to rather leech-like in shape when active, but contracted to a short, barrel-like form when disturbed". English (1955) hypothesised that it could take approximately two to three years for the larvae of *Scaptia* to complete development. The larvae are most morphologically similar to those of *Myioscaptia* as they are more slender and shorter than *Copidapha* larvae, but are distinguished by the short and thick lateral spines on the aster (Mackerras 1960, fig. 7-18, p. 9).

Remarks. *Scaptia* is recognised as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation from all remaining Scionini (Figure 1). Moreover, *Scaptia* is hereby redefined to include the Australian species (presented in SI: Species List) exclusively belonging to the former subgenus *Scaptia* (*Scaptia*), excluding those of the newly ressurected genera *Apocampta* and *Triclista*. Mackerras (1960) indicated that the Australian species *Scaptia aurinotum* Mackerras, 1960, *Scaptia barbara* Mackerras, 1960, *Scaptia limbithorax* (Macquart, 1855) and *Scaptia norrisi* Mackerras, 1960 were somewhat similar to the South American genus *Osca*, although synonymised at the time, specifically in size, oblong shape and distinct lateral fringe of dense hair present on the abdomen. These species may represent a link between the Australian and South American fauna and are therefore desired for future molecular studies.

Regarding the southeastern Australian species *S. auriflua,* the current molecular phylogenetic hypothesis for the tribe (Lessard *et al.* 2013) indicates that the

geographically disjointed Tasmanian and mainland Australian populations exhibit minimal genetic divergence, confirming that *S. auriflua* is a single species. This suggests that the island of Tasmania was colonised more recently by the species, most likely in the Pleistocene during the last glacial period occurring 9,000 to 6,500 years ago.

Genus *LEPMIA* Fairchild, 1969 stat.n.

(Figure 13)

Scaptia Walker, 1850, subgenus *Lepmia* Fairchild, 1969, p. 203. Type species *Pangonia molesta* Wiedemann, 1828, Brazil, by original designation. Coscarón & Iide (2003, p. 757); Coscarón & Papavero (1993, pp. 18, 62, 2009, pp. 9, 54-55); Fairchild (1971, p. 16); Fairchild & Burger (1994, p. 38).

Type species. *Pangonia molesta* Wiedemann, 1828 (Figure 13), Brazil, by original designation of Fairchild (1969, p. 203).

Morphological diagnosis. Moderately-sized (length 11-15.5 mm) broad and densely haired species (Figure 13), with large bulbous abdomens, moderately-sized and thick proboscis with small, reduced labella, and more bulging and less projecting face than *Parosca* or *Pseudoscione*. The genus appears to be an intermediate form of *Pseudoscione* and *Scaptia*, with a stout build, thick proboscis and robust legs of *Scaptia*, with the projecting face and longer proboscis with reduced labella similar to *Pseudoscione*. Palpi are usually short, broad, flat and usually blunt, with an extensive bare area, most similar to *Myioscaptia* and *Plinthina*.

Female. Length 11-15.5 mm. Eyes hairy. Frons narrow (index usually 2.5 to 3.6), parallel to slightly diverging, slightly raised at centre, with a slightly bulging and distinct subcallus. Face obviously bulging, only slightly projecting, with minor depressions at base and without shine. Antennal scape and pedicel small, scape only slightly wider than the length, flagellum cylindrical with eight distinct flagellomeres without projections. Palpi short, always less than the length of the flagellum and less than one third the length of the proboscis shaft, broadly trapezoidal, flattened and slightly rounded at tip, occasionally tapered at tip, always with a well-defined flat broad bare area. Proboscis moderate in length, just exceeding the length of the head, relatively slender and chitonised, with small and reduced labella, usually not exceeding the width of the proboscis shaft. Scutum without obvious vittae, distinctly covered in dense hair.

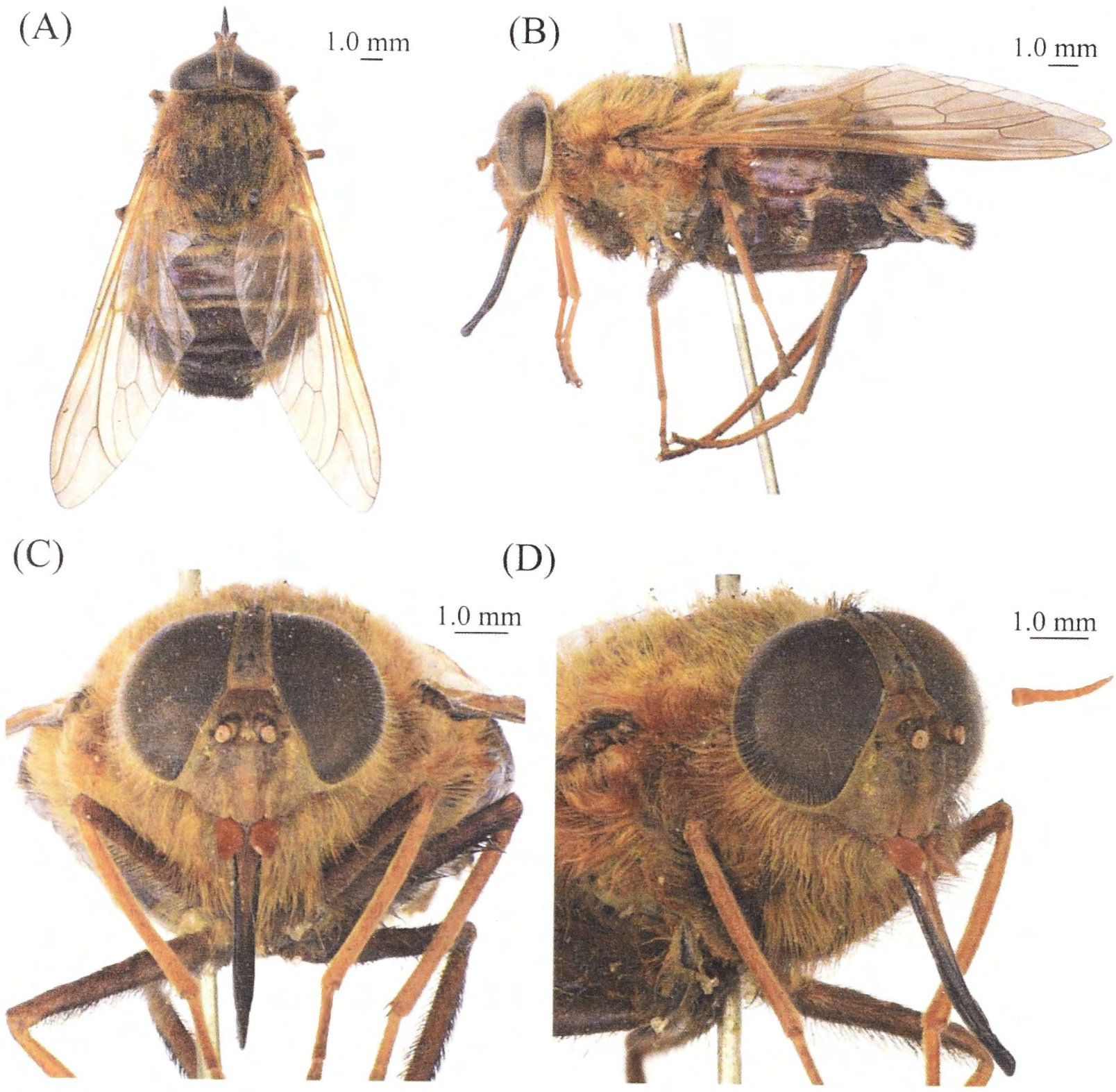

Figure 13: *Lepmia* Fairchild, 1969 **stat.n.**, female of type species *Pangonia molesta* Wiedemann, 1828: (a) dorsum; (b) side; (c) frons; (d) profile (antennal flagellum of *Diatomineura seminigra* Ricardo, 1902; NHM).

Abdomen stout and rounded, somewhat shining and without prominent markings. Wings smoky brown or grey; stigma inconspicuous; cell R_5 widely open; cell M_3 widely open; vein M_1 curved, without inflexion; R_4 angulate and without appendix. Genital cerci wider than length with a concave posterior boarder, narrow fork at base, elongated furca, and gonapophysis wider than length (Fairchild 1969; Coscarón & Iide 2003; Coscarón & Papavero 2009).

Male. Length 11 mm (based on specimens examined). Similar to female but hairier. Eyes holoptic, with upper facets not obviously enlarged (Fairchild 1969; Coscarón & Iide 2003). Coscarón & Iide (2003, pp. 757, 760) described the genitalia of *Lepmia seminigra* (Ricardo, 1902) as having the "gonocoxite a little wider than basistyle length; dististyle

pointed distally with blunt apex; aedeagus robust; epandrium elongated, gradually concave basally, ventral plate of proctiger narrow and cerci subtrapezoidal", and the genitalia of *L. molesta* as having the cercus "truncate with small median depression apically, [and] ninth tergite with long hairs". According to Wilkerson and Coscarón (1984), the male of *Lepmia leucothorax* (Ricardo, 1900) **trans.n.** has relatively shorter cerci when compared to *Pseudoscione*.

Species included. There are now six recognised species of *Lepmia* (Species List), including the four species *Lepmia atra* (Philippi, 1865) **trans.n.**, *Lepmia grisea* (Jaennicke, 1867) **trans.n.**, *Lepmia hibernus* (Wilkerson & Coscarón, 1984) **trans.n.** and *L. leucothorax,* which have been transferred from their previous position within the former subgenus *Scaptia* (*Pseudoscione*) (see Remarks).

Key to females of South American species of the revised genus *Lepmia*

1. Small species (length 11-13.5 mm); scutal hairs not overly dense; abdomen with first two tergites pale yellowish-brown, contrasting to darker brown apical tergites. Brazil..... 2

Large species (length 12-15.5 mm); scutum densely covered in yellowish-brown or grey hairs, usually contrasting ground colour; abdomen concolorous dark reddish-brown or black. Brazil and Chile..... 3

2. Scutum and abdomen rather concolorous yellow to reddish-brown, not obviously contrasting; scutal hairs copper to golden yellow..... *seminigra* (Ricardo, 1902)

Scutum dark brown to blackish, sharply contrasting the paler yellowish-brown first two anterior tergites of abdomen; scutal hairs grey to dark brown..... *hibernus* (Wilkerson & Coscarón, 1984) **trans.n.**

3. Scutum and abdomen dark brown, with yellowish to golden-brown scutal hairs; wings smoky brown. Brazil..... *molesta* (Wiedemann, 1828)

Scutum and abdomen black, with pale grey to white scutal hairs; wings smoky grey. Chile..... 4

4. Scutal hairs entirely black, occasionally mixed with grey hairs; pleural and abdominal hairs black..... *atra* (Philippi, 1865) **trans.n.**

Scutal hairs pale grey to white; pleural hairs black with pale grey to white hairs on the upper ridge of the anepisternum; abdominal hairs black, occasionally with a white tuft on first two tergites..... 5

5. Beard almost entirely black, occasionally white to grey on the posterior half; scutal hairs long..... *leucothorax* (Ricardo, 1900) **trans.n.**

Beard uniformly grey to white; scutal hairs short..... *grisea* (Jaennicke, 1867) **trans.n.**

Distribution. South America. Found in the mountainous regions of Minas Gerais, Espirito Santo, São Paulo and Rio de Janeiro, South-eastern Brazil (Lessard *et al.* 2013; Coscarón & Iide 2003). The distribution is further extended into the Atacama to Maule Provinces of Chile by the inclusion of the species previously belonging to the former subgenus *Scaptia* (*Pseudoscione*) (see Remarks).

Biology. Little is known regarding the feeding habit of the genus, although it appears to be blood-feeding since *L. molesta* and *L. hibernus* have both been reported to attack humans (Coscarón & Iide 2003; Wilkerson & Coscarón 1984). Larval stages are unknown for the genus.

Remarks. *Lepmia* is hereby raised to genus level and accepted as a valid genus of the Scionini, based on the distinct morphology and firm genetic separation from all remaining Scionini (Figure 1). The revised genus now includes the species *L. molesta, L. seminigra,* in addition to *L. atra* (Chile), *L. grisea* (Chile), *L. hibernus* (Brazil) and *L. leucothorax* (Chile) that have been removed from their previous position within the former subgenus *Scaptia* (*Pseudoscione*) and reassigned to the newly revised *Lepmia,* based on the shared similarities of the distinct broad and flattened palpi, thick proboscis with reduced labella, densely haired scutum and stout robust abdomens. Wilkerson and Coscarón (1984) alluded to *L. hibernus* as being closely related to *Lepmia* based on the coloration and markings on the scutum and abdomen. More species are desired for future molecular analysis to confirm the monophyly of the genus, since only one specimen of *L. leucothorax* was included in the current molecular phylogenetic hypothesis for the tribe (Lessard *et al.* 2013).

Genus *PAROSCA* Enderlein, 1922 stat.n.

(Figure 14)

Parosca Enderlein, 1922, p. 338. Originally listed as monotypic for *Pangonia viridiventris* Macquart, 1838, Chile, in the key to the former subfamily Melpiinae and officially described sometime after by Enderlein (1925, p. 295). Kröber (1930b, p. 127, 1932, p. 188). Reduced to a synonym of *Listrapha* Enderlein, 1922 by Kröber (1934), although *Listrapha* was already considered a synonym of *Parosca* earlier by Kröber (1930, p. 118). Both genera were eventually reduced to synonyms of *Scaptia* (*Pseudoscione*) by Mackerras (1955, p. 493) and was accepted by Fairchild (1956, p. 9; 1966a, p. 3); Wilkerson & Coscarón (1984, p. 234); Coscarón & Papavero (1993, 2009).

Listrapha Enderlein, 1922, p. 338. Type *Pangonia latipalpis* Macquart, 1850, Chile, by original designation. Enderlein (1925, p. 278); Kröber (1934). Reduced to a synonym of *Parosca* by Kröber (1930, p. 118) and was further synonymised under *Scaptia* (*Pseudoscione*) by Mackerras (1955, p. 493). Accepted by Coscarón & Papavero (1993, 2009); Fairchild (1956, p. 9; 1966a, p. 3); Wilkerson & Coscarón (1984, p. 234).

Type species. *Pangonia viridiventris* Macquart, 1838 (Figure 14), Chile, by original designation of Enderlein (1922, p. 338).

Morphological diagnosis. Medium-sized (11-16 mm) species, most similar to *Pseudoscione* sharing the conspicuously projecting face, diverging frons and long and slender proboscis, but distinguished by the broader build, the proboscis with slightly thicker labella, and the more extensively flattened palpi that are broad, triangular, dorsally rotated and slightly longer (Figure 14) than *Pseudoscione*.

Female. Length 11-16 mm. Eyes hairy. Frons narrow or wide (index usually 1.9 to 3.2), strongly diverging, not obviously raised at centre, subcallus slightly bulging and distinct. Face strongly projecting and bulging at sides and base, occasionally partially shining. Antennae scape and pedicel small, equal to thickness of cylindrical flagellum, tapering at tip, with eight distinct flagellomeres without projections. Palpi relatively short, less than or occasionally equal to the length of the flagellum and less than one third the length of the proboscis shaft, broad and almost triangular, pointed at tip, rotated dorsally, extensively flattened, with a well-defined lateral bare area. Proboscis long, approximately one and a half times the length of the head, slender and heavily chitonised, usually with moderately developed labella, slightly wider than the proboscis shaft. Scutum hairy, with at least indications of vittae. Abdomen relatively stout and rounded at tip, without prominent markings. Wings smoky grey to brown; stigma inconspicuous; cell R_5 usually

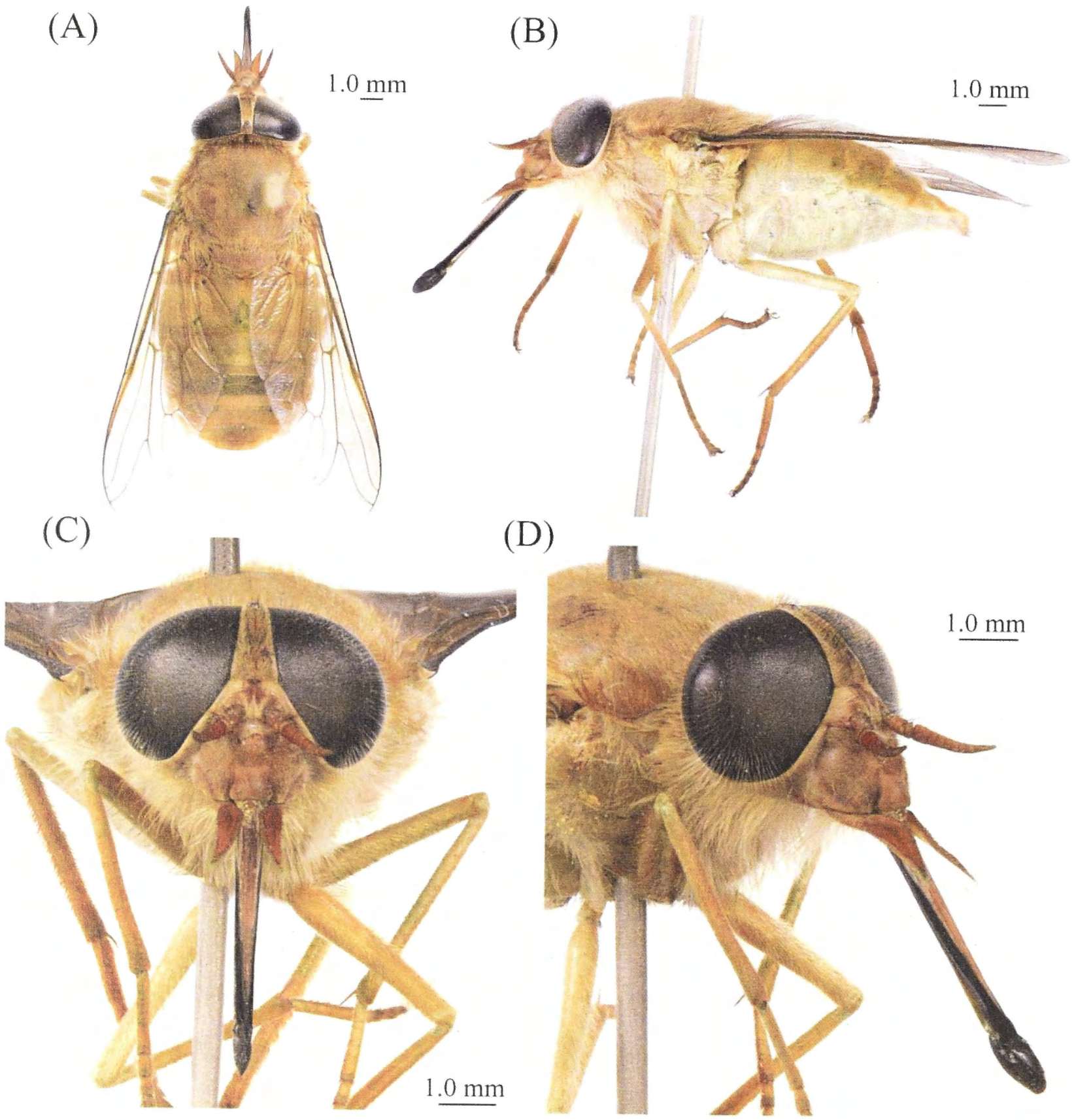

Figure 14: *Parosca* Enderlein, 1922 **stat.n.**, female of type species *Pangonia viridiventris* Macquart, 1838: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

open or narrowed, occasionally closed; cell M_3 open; vein M_1 without inflexion; vein R_4 curved or angulate, either with or without appendix (Enderlein 1925; Kröber 1932). Cerci length approximately equal to width, with a rounded border, occasionally with the cerci curved laterally and at the distal boarder (Wilkerson & Coscarón 1984).

Male. Length 12-13 mm (of specimens examined). Hairier than females, generally with a more slender proboscis. Eyes holoptic, with upper facets only slightly enlarged. Palpi short, subcylindrical, blunt and with reduced flat apical pits. Gonocoxite length

approximately equal to width at the base, with the epandrium subtrapezoidal with strongly curved cerci with a convexed boarder (Wilkerson & Coscarón 1984).

Species included. There are now three recognised species (Species List) of the newly revised genus *Parosca* (see Remarks).

Key to females of South American species of the revised genus *Parosca*

1. Abdomen dark brown to black, banded with pale posterior margins covered with pale grey hairs; scutal vittae conspicuous; legs dark red to brown..... *albifrons* (Macquart, 1838) **trans.n.**

Abdomen yellowish-green to brown, unbanded, shining and occasionally darkening distally, hairs yellow to golden-brown, occasionally mixed with black; scutal vittae less obvious; legs pale yellow to brown..... 2

2. Scutum pale green to yellowish-brown, concolorous to abdomen; abdominal hairs uniformly yellow to brown..... *viridiventris* (Macquart, 1838) **trans.n.**

Scutum dark brown to black, sharply contrasting to abdomen; abdominal hairs golden yellow, with black hairs on the distal tergite only..... *latipalpis* (Macquart, 1849) **trans.n.**

Distribution. South America. Ranging from the Atacama to Chiloe Provinces of Chile (Lessard *et al.* 2013; Wilkerson & Coscarón 1984).

Biology. The genus appears to be both blood and nectar feeding, with *Parosca viridiventris* (Macquart, 1838) **trans.n.** attracted to humans and the Myrtaceous plant genus *Luma* (Lessard & Yeates 2012b; personal observation). Larval stages are unknown for the genus.

Remarks. The taxonomy of the genus has been historically unclear, with Kröber (1932) stating that *Parosca* was ill-defined by the excessive number of heterogeneous species and limited material available for examination. Furthermore, workers were unable to agree on which species to include in the genus; the type species *Pr. viridiventris* and *Lepmia leucothorax* and *Lepmia grisea* were included in both Enderlein (1925) and Kröber's (1930b) versions of the genus, however, *Pseudoscione dorsoguttata* (Macquart, 1850), *Scaptia limbithorax* (Macquart, 1855), *Osca albithorax* (Macquart, 1838) **trans.n.** and *Osca varia* (Walker, 1848) **trans.n.** were also included in Enderlein's (1925)

definition of *Parosca*, but were replaced by Kröber (1930b) with the species *Pseudoscione vittata* (Philippi, 1865) and *Pseudoscione latipalpis* (Macquart, 1849). Given this uncertainty, Kröber (1930b) suggested that the genus might one day be resolved on the morphology of the palpi, a character that has proven useful in the currently revised definition of the genus.

Parosca is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation from all remaining Scionini (Figure 1). These results redefine the *Parosca* to include the species *Parosca albifrons* (Macquart, 1938) **trans.n.**, *Parosca latipalpis* (Macquart, 1849) **trans.n.** and *Pr. viridiventris*, which have been transferred from their previous position within the former subgenus *Scaptia* (*Pseudoscione*), based on the shared similarities of the distinct broad build, the proboscis with considerably thick labella, and moderately flattened palpi that are somewhat wide, triangular and dorsally rotated.

Genus *PSEUDOSCIONE* Lutz, 1918 stat.n.

(Figure 15)

Pseudoscione Lutz in Lutz, Araujo, and Fonseca, 1918, p. 167. Type species *Diatomineura longipennis* Ricardo, 1902, Brazil, originally presented in a checklist of regional species without a description or statement that the genus was proposed as new, formally designated as the type species by Fairchild (1950, p. 124) and described by Mackerras (1955, p. 493).

Listriosca Enderlein, 1922. Type species *Pangonia australis* (Philippi, 1865), Chile, by original designation. Reduced to a synonym of *Scaptia* (*Pseudoscione*) by Mackerras (1955, p. 493) and confirmed by Fairchild (1956, p. 9, 1966a, p. 2).

Listraphella Enderlein, 1929. Type species *Listraphella schoenemanni* Enderlein, 1929 (= *Pangonia australis* Philippi, 1865), Chile, by original designation. Reduced to a synonym of *Scaptia* (*Pseudoscione*) by Mackerras (1955, p. 493) stating the only difference to *Pseudoscione* was the uninformative presence of a short appendix to wing vein R_4. Fairchild (1956, p. 9, 1966a, p. 2); Wilkerson & Coscarón (1984, p. 217)

Scaptia Walker, 1850, subgenus *Pseudoscione* (Lutz in Lutz, Araujo, and Fonseca, 1918). Coscarón & Papavero (1993, pp. 18, 63, 2009, pp. 9, 57); Fairchild (1969, p. 203); Lessard & Yeates 2012b; Mackerras (1955, p. 493, 1957, p. 586, 1960, p. 81, 1964, p. 79); Wilkerson & Coscarón (1984, p. 213); Wilkerson & Fairchild (1984, p. 45).

Type species. *Diatomineura longipennis* Ricardo, 1902 (Figure 15), Brazil, by designation of Fairchild (1950, p. 124).

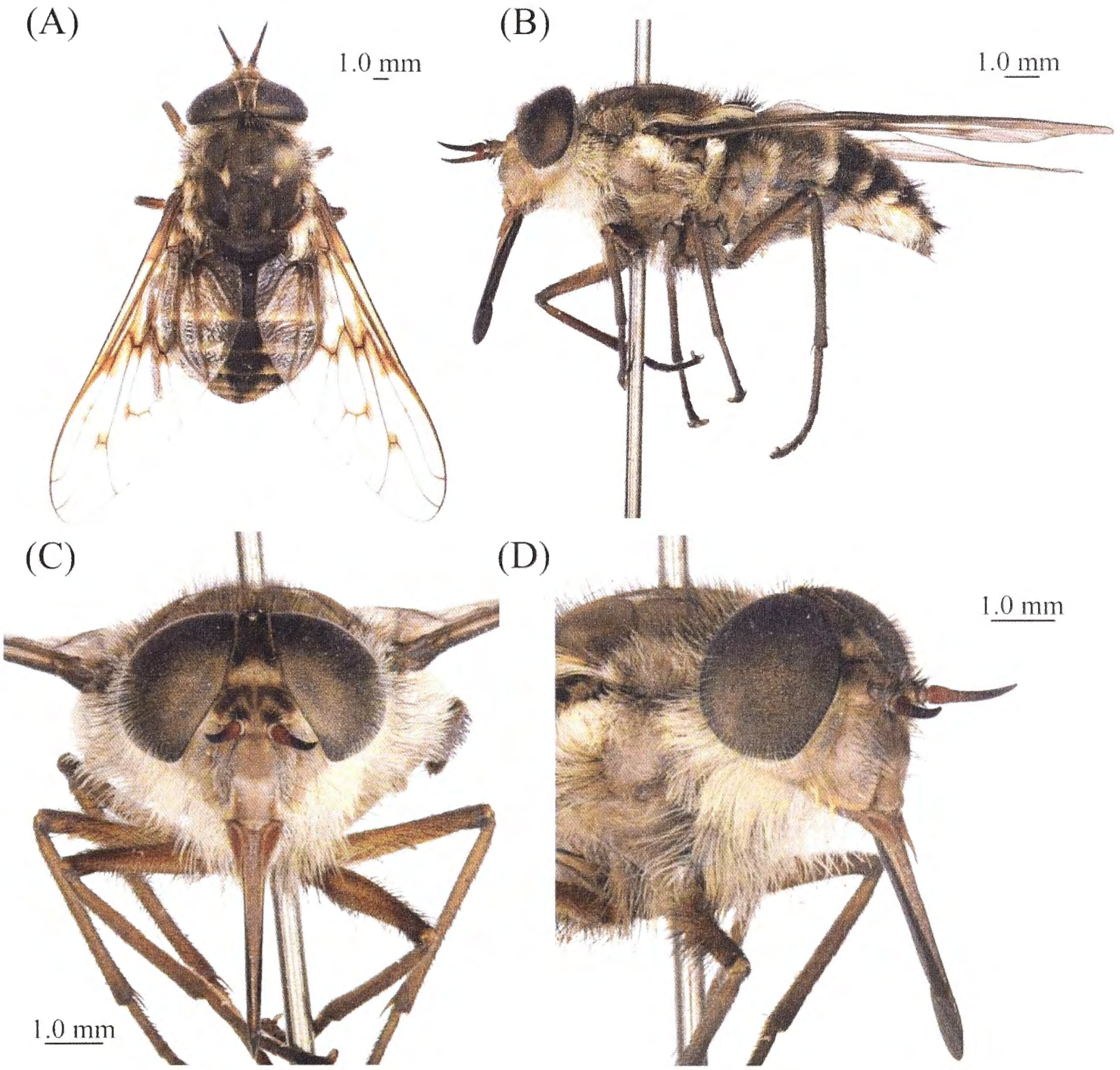

Figure 15: *Pseudoscione* Lutz, 1918 **stat.n.**, female of type species *Diatomineura longipennis* Ricardo, 1902: (a) dorsum; (b) side; (c) frons; (d) profile (NHM).

Morphological diagnosis. Small to medium-sized (8-15 length mm) stout species, with a strong resemblance to *Scione* exhibited in the pale markings along the sutures of the scutum, but distinguished by the open wing cell M_3 (Figure 15). Distinguished from *Parosca* by the slightly smaller abdomen, short and thick palpi with a prominent deep lateral bare concavity, and proboscis with reduced labella equal to the width of the proboscis shaft.

Female. Length 8-15 mm. Eyes hairy. Frons relatively wide (index usually 1.5 to 2.6), moderately diverging and hairy, flat at centre, subcallus slightly bulging and distinct. Face strongly projecting, only slightly bulging at base and sides, without shine. Antennal with small scape and pedicel, equal to the width of the cylindrical flagellum, tapering at tip,

with eight distinct flagellomeres without projections. Palpi short, less than the length of the flagellum and less than one third the length of the proboscis shaft, shape variable, usually broad and tapered with a deep well-defined bare lateral concavity. Proboscis long, at least one and a quarter times the head length, relatively slender, with small less developed labella that are generally only as wide as the proboscis shaft. Scutum with at least indications of vittae, sometimes exceeding transverse suture. Abdomen usually slender and ovular, only slightly narrowed distally, usually with indications of markings. Wings usually smoky, occasionally spotted on the crossveins; stigma inconspicuous; cell R_5 usually open; cell M_3 open; vein M_1 without inflexion; R_4 curved to angulate, with or without appendix. Female cerci usually truncate apically, length approximately equal to width, sometimes slightly wider than height, hind boarder convex or flat, genital furca shorter than above, usually strongly chitonised, with the eight sternite occasionally narrowed. (Coscarón & Papavero 2009; Mackerras 1955, 1957, 1960; Wilkerson & Coscarón 1984).

Male. Length 11-12 mm. Eyes holoptic, with upper facets not obviously enlarged. Palpi subclylindrical, usually blunt or slightly pointed at end, hairy, with a reduced apical pit or bare area. Genitalia with gonocoxite never exceeding the width of the base, epandrium subtrapezoidal, with strongly curved cerci and convexed boarder (Wilkerson & Coscarón 1984).

Species included. A valid key to all nine recognised species of *Pseudoscione* (Species List) was provided by Wilkerson and Coscarón (1984) in the form of the previous subgenus *Scaptia* (*Pseudoscione*), excluding the former species now transferred to the newly revised genera *Lepmia* (*L. atra, L. grisea, L. hibernus* and *L. leucothorax*) and *Parosca* (*Pr. albifrons, Pr. latipalpis* and *Pr. viridiventris*) (see Remarks).

Distribution. South America. Predominantly Patagonian, ranging from the Atacama to Aisén Provinces of Chile and expanding eastwards to the Catamarca, Misiones Provinces and the southern Chubut Province of Argentina. The genus is also found in the Minas Gerais and Sao Paulo Regions of Brazil (Lessard *et al.* 2013; Wilkerson & Coscarón 1984).

Biology. Currently there are limited records for the feeding behaviour of the genus, although *Ps. australis* (Philippi, 1865) is known to attack humans and is a suspected blood-feeder (personal communication). Larval stages are unknown for the genus.

Remarks. *Pseudoscione* is hereby reinstated as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation from all remaining Scionini (Figure 1). The revised genus now comprises nine species (presented in SI: Species List), as some species previously included in the former subgenus *Scaptia* (*Pseudoscione*) were reassigned herein to the newly revised genera *Lepmia* (*L. atra, L. grisea, L. hibernus,* and *L. leucothorax*) and *Parosca* (*Pr. albifrons, Pr. latipalpis* and *Pr. viridiventris*), based on morphological similarities in the form of the palpi and proboscis (see relevant genera above). The type species *Ps. longipennis* is desired for future phylogenetic studies.

Genus *SCIONE* Walker, 1850

(Figure 16)

Scione Walker, 1850, p. 10. Originally monotypic for *Pangonia incompleta* Macquart, 1845, South America. Burger (2002, p. 931); Cárdenas *et al.* (2009); Chainey *et al.* (1994, pp. 326, 327); Coscarón & Papavero (1993, pp. 18, 64, 2009, pp. 9, 58-59); Fairchild (1942, p. 184, 1953a, 1966b, p.355, 1967a, p. 92, 1969, p. 203, 1971, p. 25); Kröber (1930a); Mackerras (1955, p. 486); Philip (1967, p. 111); Szilády (1926, p. 27); Wilkerson (1979); Wilkerson & Fairchild (1984, p. 45).

Diclista Schiner, 1867, p. 305. Monotypic for *Pangonia incompleta* Macquart, 1845, South America, by original designation. Synonymy by Fairchild (1942, p. 184); Mackerras (1955, p. 486) and Fairchild (1971, p. 25).

Rhinotriclista Enderlein, 1922, p. 338. Type *Diclisa maculipennis* Schiner, 1868, Colombia, by original designation. Synonymised by Kröber (1932) and accepted by Fairchild (1942, p. 184, 1971, p. 25) and Mackerras (1955, p. 486).

Type species. Originally monotypic for *Pangonia incompleta* Macquart, 1845 (Figure 16), South America, by original designation of Walker (1850, p. 10).

Morphological diagnosis. Rather small (length 9-16 mm) and slender uniformly mottled species, with an obviously projecting face, proboscis with small, undeveloped labella, strong scutal and abdominal vittae, slender legs, and wings with obvious cloudy markings

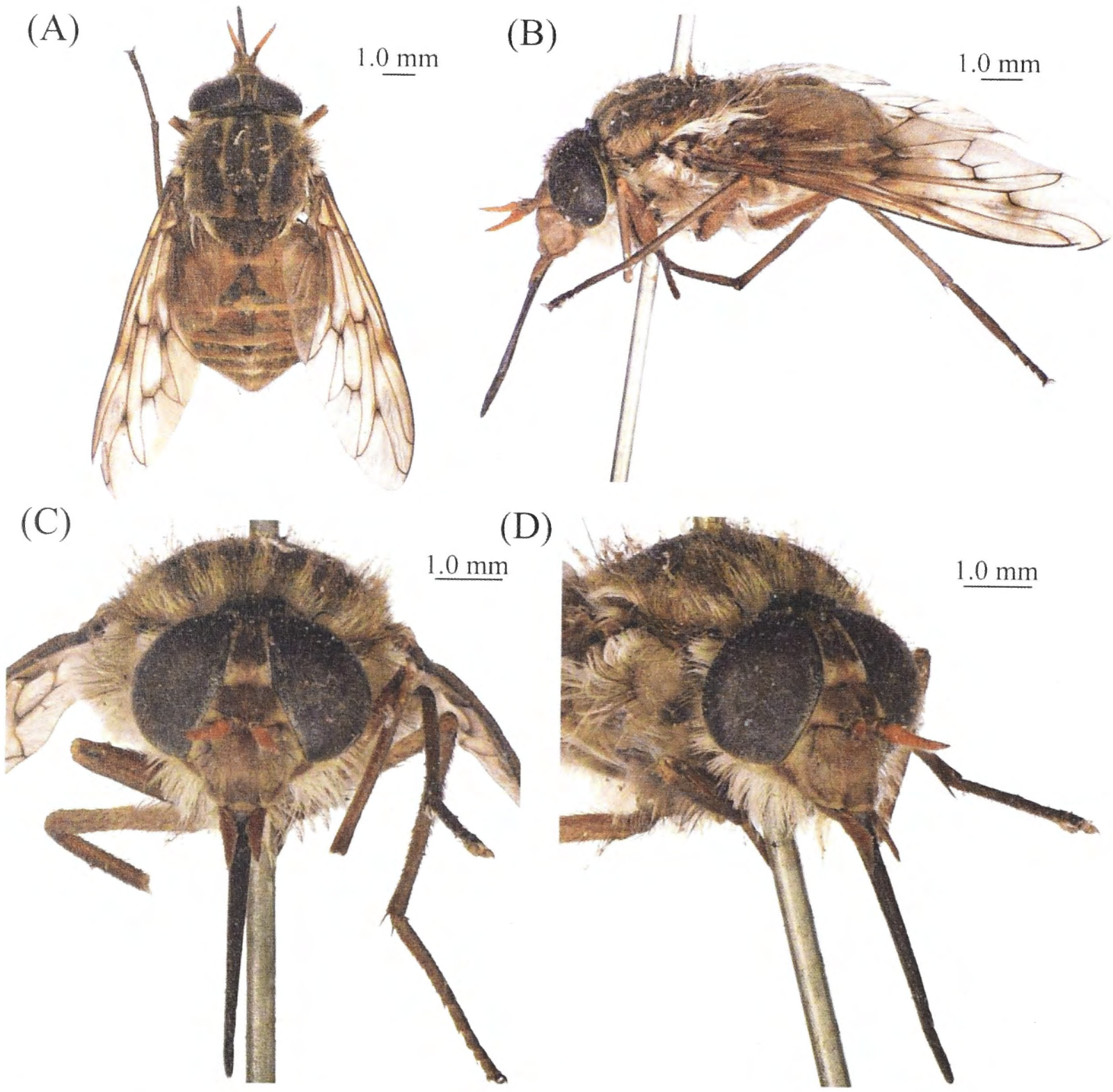

Figure 16: *Scione* Walker, 1850, female of type species *Pangonia incompleta* Macquart, 1845: (a) dorsum; (b) side; (c) frons; (d) profile (NHM).

on crossveins (Figure 16). Distinguished from *Fidena* and *Pseudoscione* by the smaller size and closure of the wing cells R_5 and M_3.

Female. Length 9-16 mm (based on specimens examined). Eyes hairy. Frons wide (index usually 1.8 to 3.3), usually diverging although sometimes parallel, occasionally only slightly raised at centre, usually with a distinct subcallus that is somewhat projecting. Face moderate to considerably projecting or conical and without shine. Antennal scape and pedicel short, equal to the width of the cylindrical flagellum with eight distinct flagellomeres without projections. Palpi either long, equal to the length of the flagellum, flat and extremely tapered, or short, less than the length of the flagellum, broad and leaf-like, almost always less than a quarter the length of the proboscis, and with a distinct

lateral bare area. Proboscis long, greater than one and a quarter times the length of the head, sometimes longer than both the head and thorax, slender and heavily chitonised, with small, undeveloped labella, narrower than the proboscis shaft. Scutum usually heavily patterned with conspicuous scutal vittae exceeding the transverse suture. Abdomen ovular to slender, and narrowed at apices, usually with distinct markings or medial patches of white hairs. Wings generally smoky greyish to brown, usually spotted at cross veins, sometimes clear; stigma inconspicuous; cell R_5 and M_3 closed and generally petiolate, occasionally with vein M_2 failing to touch the edge of the wing; vein M_1 without inflexion; R_4 curved to angulate, with or without appendix. Female genitalia with the furca usually without projections, although projections can occasionally be very small. (Fairchild 1942; Mackerras 1955; Coscarón & Papavero 2009).

Male. Smaller than females, length 11 mm (based on specimens examined). Eyes holoptic, with upper facets only slightly enlarged. Palpi hairy, subcylindrical and blunt at tip, with reduced apical pits. Mackerras (1955, p. 487) stated there is nothing informative in the male hypopygium although it is similar to *Pseudoscione*.

Species included. The genus includes 41 recognised species (Species List). The diagnostic key to the species of *Scione* has not been updated since the work of Kröber (1930a), which included only 25 known species at the time. Two smaller keys were also published by Szilády (1926) and Fairchild's (1942), including 19 and four species, respectively.

Distribution. Central and South America. Ranging from Mexico, Guatemala and Panama to Colombia, Venezuela, Ecuador, Brazil, Peru, Bolivia and Argentina (Fairchild 1942; Lessard *et al.* 2013; Mackerras 1955).

Biology. The genus appears to be blood-feeding, with *Scione aurulans* (Fairchild 1953a), *Scione ablusus* Fairchild, 1964 and *Scione flavohirta* Ricardo, 1902 all recorded to feed on humans, with the latter also recorded to feed on cattle (Chainey *et al.* 1994; Fairchild 1964). Larval stages are unknown for the genus.

Remarks. *Scione* is accepted as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation from all remaining Scionini (Figure 1). The genus is considered to be a taxonomically difficult group, given

the large morphological uniformity of species and lack of useful descriptive characters and has not been formally revised in over 80 years. Fairchild (1942, p. 185) stated that *Scione* was in "great need of revision" as that the majority of earlier descriptions were "nearly worthless", and that the only attempt so far made by Kröber (1930a) was unsuccessful. Moreover, the key to species strongly warrants updating and should include the recently described species that have accumulated since Kröber's (1930a) work, as well as addressing any potential synonymies. Therefore, more extensive sampling of material, including the type species, is desired for future molecular phylogenetic and taxonomic studies of the genus.

Genus *FIDENA* Walker, 1850

(Figure 17)

Fidena Walker, 1850, p. 8. Type *Pangonia leucopogon* Wiedemann, 1828, Brazil, by designation of Coquillett, 1910. Chainey *et al.* (1994, pp. 325, 326); Fairchild (1941, p. 639, 1953b, p. 206, 1966b, p.346, 1967a, p. 85, 1969, p. 203, 1971, p. 16); Kröber (1933, p. 238); Mackerras (1955, p. 487); Philip (1967, p. 106); Wilkerson & Fairchild (1984, p. 45).

Melpia Walker, 1850, p. 8. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Coquillett, 1910. Synonymy suggested by Kröber (1930b, p. 130, 1932, p. 187). Mackerras (1955) agreed upon examination of type species and affirmed that *Fidena* had priority. Fairchild (1956, p. 9).

Erephopsis Rondani, 1863. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Coquillett (1910). Synonymy by Mackerras (1955, p. 487).

Sackenimyia Bigot, 1879. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Enderlein (1925). Synonymy by Mackerras (1955, p. 487).

Phaeoneura Lutz, 1909. Monotypic for *Pangonia basilaris* Wiedemann, 1828, Brazil. Synonymy by Enderlein (1925).

?Bombylopsis Lutz, 1909. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild 1950. Synonymy by Kröber (1934). Mackerras (1955, p. 488).

Epipsila Lutz, 1909. Type *Epipsila eriomeroides* Lutz, 1909, Brazil, be designation of Enderlein 1925. Synonymy by Enderlein (1925).

Ionopsis Lutz, 1909. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Enderlein 1925. Synonymy by Mackerras (1955, p. 488).

Neopangonia Lutz, 1909. Monotypic for *Neopangonia pusilla* Lutz, 1909, Brazil. Recognised as a subgenus of *Fidena* by Enderlein (1925).

Bombylomyia Lutz, 1911. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild (1950). Synonymy by Mackerras (1955, p. 488).

Bombylomorpha Lutz, 1911. Monotypic for *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild (1950). Synonymy by Mackerras (1955, p. 488).

Laphriomyia Lutz, 1911. Monotypic for *Laphriomyia mirabilis* Lutz, 1911, Brazil. Synonymy by Mackerras (1955, p. 488) who stated its placement within *Fidena* was "not distinguishable from description". Recognised as a subgenus of *Fidena* by Fairchild (1966a, p. 2; 1971, p. 24). Coscarón & Papavero (1993, pp. 19, 66, 2009, pp. 10, 61).

Micropangonia Lutz, 1922. Type *Neopangonia pusilla* Lutz, 1909, Brazil, by designation of Fairchild (1950). Synonymy by Mackerras (1955, p. 488).

Leptofidena Kröber, 1930b. Monotypic for *Leptofidena beelzebul* Kröber, 1930b, Argentina, (= *Pangonia morio* Wulp, 1881), by original designation. Mackerras (1955, p. 458). Recognised as a subgenus of *Fidena* by Fairchild (1967, p. 249; 1969).

Type species. Type species *Pangonia leucopogon* Wiedemann, 1828 (Figure 17), Brazil, by designation of Coquillett (1910).

Morphological diagnosis. Medium to large (length 11-22 mm) stout species with a particularly produced snout-like and shining face, as well as an extremely long and slender proboscis with conspicuously reduced labella (Figure 17). Most similar to *Pityocera,* but distinguished by the larger size and antennal flagellum without obvious projections or prominent tufts of hair. Distinguished from *Scione* by the slender knife-like palpi and widely open wing cell M_3.

Female. Length 11-22 mm. Eyes hairy. Frons usually very narrow (index 1.9 to 5.1), parallel to slightly diverging, occasionally raised at centre, subcallus bulging and distinctly separate. Face conically produced, snout-like and shining. Antennal scape and pedicel small, equal to the width of the flagellum, slender and cylindrical, with eight distinct flagellomeres without projections. Palpi usually long, equal to length of the flagellum and less than one third the length of the proboscis shaft, occasionally broad and shorter than the length of the flagellum, usually extremely slender, flattened, tapering and knife-like, with a slender lateral bare area, often rotated dorsally. Proboscis long, exceeding the length of both the head and thorax, sometimes longer than the entire body, not heavily chitonised, with small, undeveloped labella, narrower than the proboscis shaft. Scutum usually with at least indications of vittae, occasionally covered with dense hairs. Abdomen large and usually rounded, without distinct patterns or markings. Wings smoky greyish to brown; stigma inconspicuous; cell R_5 usually closed or narrowed; cell M_3 widely open; vein M_1 without inflexion; vein R_4 angulate with or without short appendix (Coscarón & Papavero 2009; Mackerras 1955). Mackerras (1955, p. 489) described the genitalia as having the "hypopygium without distinctive characters; gonopophyses large and rounded; cerci rather truncate apically; caudal ends of

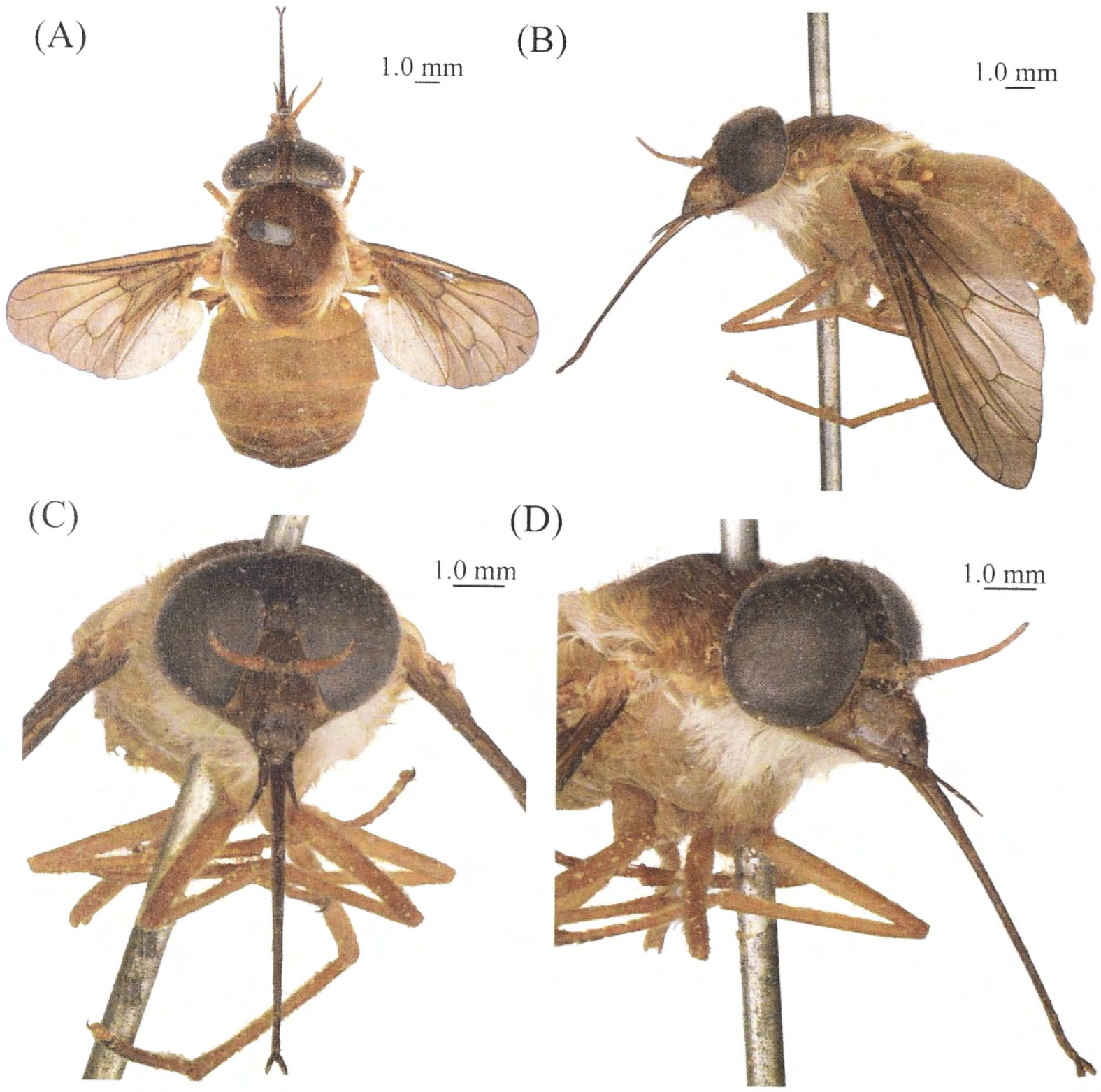

Figure 17: *Fidena* Walker, 1850, female of type species *Pangonia leucopogon* Wiedemann, 1828: (a) dorsum; (b) side; (c) frons; (d) profile (NHM).

spermathecal ducts slender, simple, moderately chitonised tubes, which can easily be seen by ordinary transmitted light".

Male. Length 12 mm (based on specimens examined). Eyes large, very densely hairy, holoptic, with the upper facets only slightly enlarged. Palpi relatively short, cylindrical at base and slender, flat and tapered at tip, with a well-developed narrow bare apical area. Mackerras (1955, p. 489) stated the hypopygium was without distinctive features.

Subgenera. The genus contains 99 described species and is further divided into four subgenera, including *Fidena* (*Fidena*) Walker, 1850 (94 spp.), *Fidena* (*Laphriomyia*)

Lutz, 1911 (3 spp.), *Fidena* (*Leptofidena*) Kröber, 1930b (monotypic), and *Fidena* (*Neopangonia*) Lutz, 1909 (monotypic).

Distribution. Widespread in South America, predominantly Brazilian, with a smaller radiation into Central America (Coscarón & Papavero 2009; Fairchild 1971; Lessard *et al.* 2013; Mackerras 1955).

Biology. The genus is blood-feeding in nature, with *Fidena* (*Fidena*) *trapidoi* Fairchild, 1953, *Fidena* (*Fidena*) *trinidadensis* Fairchild & Aitken, 1960, and *Fidena* (*Fidena*) *rhinophora* Bellardi, 1859 (under the synonym *Fidena pyrausta* Osten Sacken, 1886) all recorded to attack humans (Fairchild 1951, 1953b; Fairchild & Aitken 1960), and *Fidena* (*Fidena*) *schildi* (Hine, 1925) is known to feed on domestic pigs (Fairchild 1951). Curiously, one specimen of *Fidena* (*Fidena*) *flavipennis* Kröber, 1931 (under synonym *Fidena isthmiae* Fairchild, 1941) was recorded to feed on a captive species of *Boa* (Fairchild 1941, p. 642) and is the only known record of reptile feeding for the tribe. Mackerras (1955) mentioned that Fairchild reported some species of *Fidena* to coil the labium within the head capsule to expose the shorter piercing mouthparts for feeding on what is assumed to be animals. He also draws a parallel to the feeding strategy of the Asian Pangoniinae genus *Philoliche* (Wiedemann, 1820), which bends its labium to the side when blood-feeding. Although unrecorded, *Fidena* is expected to have a strong association with flower feeding of deep-throated flowers, similar to the Philolichini, given the significantly elongated and slender proboscis. Larval stages are currently unknown for the genus.

Remarks. *Fidena* is accepted as a valid genus of the Scionini, based on the distinct morphology, well-supported monophyly and firm genetic separation from all remaining Scionini (Figure 1). A formal taxonomic revision of *Fidena* is strongly warranted, including the key to species which should be updated to accommodate the recently described and synonymised species since the outdated work of Kröber (1933; key to only 48 species) and Fairchild (1941, 1953b; key to a maximum of nine species). Unfortunately, the phylogenetic relationships of the subgenera were not assessed in the current molecular phylogenetic hypothesis for the Scionini (Lessard *et al.* 2013), due to the limited sampling of species from the subgenus *Fidena* (*Fidena*). Therefore, more extensive sampling of each of the subgenera, including the type species, is required for future morphological and molecular studies.

Chapter Eight

Subgenus *FIDENA* Walker, 1850

(Figure 17)

Fidena Walker, 1850, p. 8. Type *Pangonia leucopogon* Wiedemann, 1828, Brazil, by designation of Coquillett, 1910. Chainey *et al.* (1994, pp. 325, 326); Fairchild (1967a, p. 85-89, 1969, p. 203, 1971, p. 16); Fairchild & Rafael (1985); Kröber (1933, p. 238); Mackerras (1955, p. 487); Philip (1967, p. 106); Wilkerson & Fairchild (1984, p. 45).

Melpia Walker, 1850, p. 8. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Coquillett, 1910. Synonymy by Kröber (1930b, p. 130, 1932, p. 187) and adopted by Mackerras (1955) who agreed upon examination of type species and affirmed that *Fidena* had priority.

Erephopsis Rondani, 1863. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Coquillett (1910). Synonymy by Mackerras (1955, p. 487).

Sackenimyia Bigot, 1879. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Enderlein (1925). Synonymy by Mackerras (1955, p. 487).

Phaeoneura Lutz, 1909. Monotypic for *Pangonia basilaris* Wiedemann, 1828, Brazil. Synonymy by Enderlein (1925).

?Bombylopsis Lutz, 1909. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild 1950. Synonymy by Kröber (1934). Mackerras (1955, p. 488).

Epipsila Lutz, 1909. Type *Epipsila eriomeroides* Lutz, 1909, Brazil, be designation of Enderlein 1925. Synonymy by Enderlein (1925).

Ionopsis Lutz, 1909. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Enderlein 1925. Synonymy by Mackerras (1955, p. 488).

Bombylomyia Lutz, 1911. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild (1950). Synonymy by Mackerras (1955, p. 488).

Bombylomorpha Lutz, 1911. Monotypic for *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild (1950). Synonymy by Mackerras (1955, p. 488).

Fidena Walker, 1850, subgenus *Fidena* Walker, 1850. Type species *Pangonia leucopogon* Wiedemann, 1828, Brazil, by designation of Coquillett, 1910. Reduced to subgenus by Fairchild (1969, p. 203, 1971, p. 17) and accepted by Burger (2002, p. 928); Cárdenas *et al.* (2009); Chainey *et al.* (1994, p. 325); Coscarón & Papavero (1993, pp. 19, 68, 2009, pp. 10, 63-64); Wilkerson & Fairchild (1984, p. 45).

Type species. *Pangonia leucopogon* Wiedemann, 1828 (Figure 17), Brazil, by designation of Coquillett (1910).

Morphological diagnosis. Length 11-22 mm. Differentiated from other subgenera by the flattened palpi, frons without subcallus, scutum without strong vittae, femora and tibiae without conspicuously long hairs, and wings with cell R_5 usually closed and without a long petiole (Coscarón & Papavero 2009).

Species included. The subgenus includes 94 recognised species (Species List).

Distribution. Central and South America. Predominantly Brazilian, ranging from Colombia, Venezuela, Suriname and Ecuador to Peru, Bolivia, Paraguay, Uruguay, Chile and Argentina, with a smaller expansion into Panama, Costa Rica and Mexico (Mackerras 1955; Coscarón & Papavero 2009).

Subgenus *LAPHRIOMYIA* Lutz, 1911

Laphriomyia Lutz, 1911, p. 71. Originally monotypic for *Laphriomyia mirabilis* Lutz, 1911. Fairchild (1950, p. 122).

Fidena Walker, 1850, subgenus *Laphriomyia* Lutz, 1911. Recognised as a subgenus of *Fidena* by Fairchild (1966a, p. 2). Chainey *et al.* (1994, pp. 325, 326); Coscarón & Papavero (1993, pp. 19, 66, 2009, pp. 10, 61); Fairchild (1969, p. 203, 1971, p. 24); Wilkerson & Fairchild (1984, p. 45).

Type species. *Laphriomyia mirabilis* Lutz, 1911, Brazil, by original designation.

Morpholgical diagnosis. Coscarón and Papavero (2009) indicated that the subgenus is distinguished by the femora and tibiae being densely covered in long and conspicuous hairs (Coscarón & Papavero 2009, p. 10).

Species included. There are three recognised species in the subgenus (Species List).

Distribution. South America. Peru, Bolivia and Brazil (Coscarón & Papavero 2009).

Subgenus *LEPTOFIDENA* Kröber, 1930

Leptofidena Kröber, 1930b, p. 134. Monotypic for *Leptofidena beelzebul* Kröber, 1930b, (= *Pangonia morio* Wulp, 1881), Argentina, by original designation. Fairchild (1967b, p. 249); Mackerras (1955, p. 458).

Fidena Walker, 1850, subgenus *Leptofidena* Kröber, 1930b. Recognised as a subgenus of *Fidena* by Fairchild (1969, p. 204, 1971, p. 25) and adopted by Coscarón & Papavero (1993, pp. 19, 67, 2009, pp. 10, 62).

Type species. Monotypic for *Leptofidena morio* Wulp, 1881, Argentina, by original designation (under synonym *Leptofidena beelzebul* Kröber, 1930b).

Morphological diagnosis. This small (length 11 mm) monotypic subgenus is diagnosed by the thick, swollen and sometimes shining palpi with a deep lateral concavity, frons with a basal callus-like protuberance, scutum without strong vittae, and closure of the wing cell R_5 with a long petiole (Coscarón & Papavero 2009; Mackerras 1955).

Species included. The subgenus is represented by the type species only (Species List).

Distribution. South America. Northwest Argentina (Coscarón & Papavero 2009).

Subgenus *NEOPANGONIA* Lutz, 1909

Neopangonia Lutz, 1909, p. 651. Monotypic for *Neopangonia pusilla* Lutz, 1909, Brazil, by original designation.

Neopangonia Lutz, 1909, subgenus *Micropangonia* Lutz, 1922, p. 5. Type species *Neopangonia pusilla* Lutz, 1909, Brazil, by designation of Fairchild (1950, p. 123). Synonymised by Mackerras (1955, p. 488).

Fidena Walker, 1850, subgenus *Neopangonia* Lutz, 1909. Recognised as a subgenus of *Fidena* by Enderlein (1925). Coscarón & Papavero (1993, pp. 19, 65, 2009, pp. 9, 60); Fairchild (1969, p. 203, 1971, p. 24).

Type species. Monotypic for *Neopangonia pusilla* Lutz, 1909, Brazil, by original designation.

Morphological diagnosis. A small monotypic subgenus distinguished by the hairy face with many conspicuous long hairs, strongly patterned scutum with obvious vittae, and wings with cell R_5 broadly open (Coscarón & Papavero 2009).

Species included. The subgenus is represented by the type species only (Species List).

Distribution. South America. Southeastern Brazil (Coscarón & Papavero 2009).

Genus *PITYOCERA* Giglio-Tos, 1896

(Figure 18)

Pityocera Giglio-Tos, 1896. Originally monotypic for *Pityocera festae* Giglio-Tos, 1896, Panama. Kröber (1930c, p. 310); Chainey *et al.* (1994, p. 326); Coscarón & Papavero (1993, 2009); Fairchild (1942, p. 183, 1969, p. 203); Mackerras (1955, p. 485); Wilkerson & Fairchild (1984, p. 45).

Pseudelaphella Kröber, 1930c, p. 305. Type species *Pangonia nana* Walker, 1850, Brazil, by original designation. Suppressed as a subgenus of *Pityocera* by Fairchild (1966b, p. 332; 1969, p. 203, 1971, p. 27).

Elaphella Bezzi, 1913 and Mackerras 1955, p. 486. Monotypic for *Pangonia cervus* Wiedemann, 1828, Brazil, by original designation. Provided as a replacement name for *Dicrania* Macquart, 1834 by Mackerras (1955, p. 486). Kröber (1930c, p. 309). Suppressed as a subgenus of *Pityocera* by Fairchild (1969, p. 204, 1971, p. 27).

Type species. *Pityocera festae* Giglio-Tos, 1896 (Figure 18), Panama, by original designation.

Morphological diagnosis. Small to medium-sized (length 8-14 mm) concolorous brown species, with an obviously projecting and shining face, slender knife-like palpi, and proboscis equal to or greater than the length of the body, most similar to *Fidena*, but distinguished by the smaller size, antennal flagellum with obvious projections or prominent tufts of hairs on one or more flagellomeres, and the inflexed curvature of the M_1 wing vein (Figure 18).

Female. Length 8-14 mm. Eyes hairy. Frons narrow (index usually 2.5 to 4.8), slightly diverging ventrally, flat at centre, with distinct projecting subcallus. Face conically produced and snout-like, conspicuously shining. Antennal scape and pedicel small, flagellum with obvious structural projections or tufts of conspicuous hairs on one or more of the seven to eight distinct flagellomeres, sometimes with the apical two flagellomeres fused. Palpi long, equal to the length of the flagellum, narrow and extremely tapered, almost knife-like, with a flat slender bare area that is dorsally rotated. Proboscis long, exceeding the length of both the head and thorax, sometimes longer than the entire body, not heavily chitonised, with a small undeveloped labellum that is narrower than the proboscis shaft. Scutum with at least indications of vittae. Abdomen ovular and rounded at end, without prominent markings. Wings smoky brown; stigma inconspicuous; cell R_5 closed, with exceedingly long petiole; cell M_3 widely open; vein M_1 with an inflexion or anterior bending towards vein R_5; R_4 angulate to curved, without appendix. Female genital

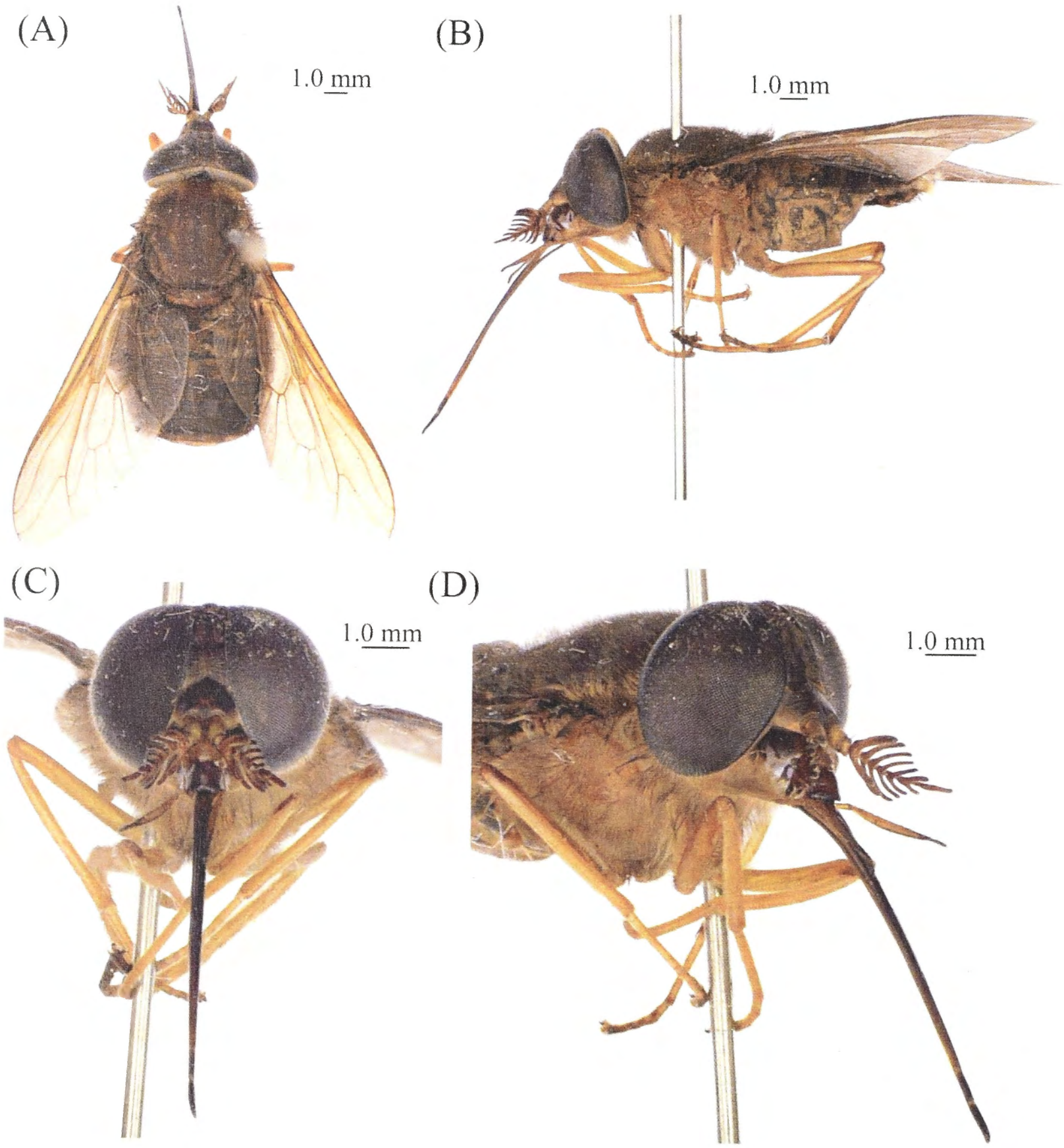

Figure 18: *Pityocera* Giglio-Tos, 1896, female of type species *Pityocera festae* Giglio-Tos, 1896: (a) dorsum; (b) side; (c) frons; (d) profile (NHM).

furca with basal projection, hypopygium indistinctive (Fairchild 1942, 1969; Mackerras 1955; Coscarón & Papavero 2009).

Male. Length 11-13 mm. Eyes holoptic, with upper facets slightly enlarged. Palpi short, cylindrical at base, remainder slender and flat, with a distinct lateral flat bare area. Genitalia are unrecorded.

Subgenera. The genus contains five described species and is further divided into three subgenera, including *Pityocera* (*Pityocera*) Giglio-Tos, 1896 (monotypic), *Pityocera*

(*Elaphella*) Bezzi, 1913 (monotypic), and *Pityocera* (*Pseudelaphella*) Kröber, 1930c (3 spp.).

Distribution. Central and northern South America (Coscarón & Papavero 2009; Lessard *et al.* 2013).

Biology. The genus is blood-feeding, with *Pityocera* (*Pityocera*) *festae* Giglio-Tos, 1896 recorded to feed on humans (Fairchild 1942). Larval stages are unknown for the genus.

Remarks. *Pityocera* is accepted as a valid genus of the Scionini, based on the distinct morphology and strong genetic divergence from all remaining Scionini (Figure 1). The current molecular phylogenetic hypotheis for the tribe confirms the placement of *Pityocera* within the Scionini (Lessard *et al.* 2013), instead of in a separate tribe as previously proposed by Kröber (1932). Unfortunately, the phylogenetic relationships of the subgenera for the genus are unknown due to the limited sampling of taxa, as only one species was included in the current molecular analysis. Therefore, more extensive sampling of the subgenera of *Pityocera*, including the type species, is desired for future morphological and molecular studies.

Subgenus *PITYOCERA* Giglio-Tos, 1896

(Figure 18)

Pityocera Giglio-Tos, 1896. Monotypic for *Pityocera festae* Giglio-Tos, 1896, Panama, by original designation. Enderlein (1922, p. 339); Kröber (1930c, p. 310); Fairchild (1942); Mackerras (1955, p. 485); Coscarón & Papavero (1993, 2009).

Pityocera Giglio-Tos, 1896, subgenus *Pityocera* Giglio-Tos, 1896. Suppressed as a subgenus of *Pityocera* by Fairchild (1942, p. 183, 1969, p. 203, 1971, p. 27) and accepted by Cárdenas *et al.* (2009); Coscarón & Papavero (1993, pp. 19, 71, 2009, pp. 10, 65).

Type species. Monotypic for *Pityocera festae* Giglio-Tos, 1896 (Figure 18), Panama, by original designation.

Morphological diagnosis. Length 12 mm. Diagnosed by the first six antennal flagellomeres with long projections on both the dorsal and ventral surfaces, noticeably

decreasing in size, with a shortened seventh flagellomere often fused to the eighth which is longer and finger-like (Coscarón & Papavero 2009).

Species included. The subgenus is represented by the type species only (Species List).

Distribution. Central and South America. Panama to Ecuador (Mackerras 1955; Coscarón & Papavero 2009).

Subgenus *ELAPHELLA* Bezzi, 1913

Dicrania Macquart, 1834. Type species *Pangonia cervus* Wiedemann, 1828, Brazil, by original designation. Preoccupied name of Lepeletier and Serville, 1828 (Mackerras 1955).

Elaphella Bezzi, 1913. Monotypic for *Pangonia cervus* Wiedemann, 1828, Brazil, by original designation. Provided as a replacement name for *Dicrania* Macquart, 1834 (Mackerras 1955, p. 486). Kröber (1930c, p. 309).

Diplocus Blanchard, 1845. Proposed to replace Macquart's preoccupied name for *Dicrania* Macquart, 1834, as Mackerras (1955, p. 486) stated that this genus should have had priority if it were not for the oversight of the well-used name *Ellaphella* and was consequently suppressed.

Dicranomyia Hunter, 1900, misapplied name of Stephens (1829) and proposed to replace Macquart's preoccupied name for *Dicrania* Macquart, 1834 (Mackerras 1955).

Allodicrania Enderlein, 1913. Proposed to replace Macquart's preoccupied name for *Dicrania* Macquart, 1834 (Mackerras 1955).

Stichocera Hine, 1920. Proposed to replace Macquart's preoccupied name for *Dicrania* Macquart, 1834 (Mackerras 1955).

Pityocera Giglio-Tos, 1896, subgenus *Elaphella* Bezzi, 1913. Suppressed as a subgenus of *Pityocera* by Fairchild (1969, p. 204, 1971, p. 27) and accepted by Cárdenas *et al.* (2009); Chainey *et al.* (1994, p. 326); Coscarón & Papavero (1993, pp. 19, 70-71, 2009, pp. 10, 66); Wilkerson & Fairchild (1984, p. 45).

Type species. Monotypic for *Pangonia cervus* Wiedemann, 1828, Brazil, by original designation of Bezzi (1913).

Morphological Diagnosis. Length 12-14 mm. Similar to *Pityocera* (*Pityocera*) but differentiated by the long projections limited to the dorsal surface of the second to sixth antennal flagellomeres, with the first flagellomere long, forwardly projecting and finger-like, the remainder of flagellomere projections smaller and decreasing in size towards tip, with the seventh and eight flagellomeres fused (Mackerras 1955; Coscarón & Papavero

2009). Mackerras (1955) also mentioned the presence of a stump vein on the M_1 on the wing.

Species included. The subgenus is represented by the type species only (Species List).

Distribution. South America. Predominantly northern, ranging from Suriname and French Guiana to Brazil and Peru (Mackerras 1955; Coscarón & Papavero 2009).

Subgenus *PSEUDELAPHELLA* Kröber, 1930

Pseudelaphella Kröber, 1930c, p. 305. Type species *Pangonia nana* Walker, 1850, Brazil, by original designation.

Pityocera Giglio-Tos, 1896, subgenus *Pseudelaphella* Kröber, 1930c. Recognised as a subgenus of *Pityocera* by Fairchild (1966b, p. 332; 1969, p. 203, 1971, p. 27). Cárdenas *et al.* (2009); Chainey *et al.* (1994, p. 326); Coscarón & Papavero (1993, pp. 19, 70-71, 2009, pp. 10, 65).

Heteroscena Campos, 1952, p. 104. Type species *Pangonia nana* Walker, 1850, synonymised by Fairchild (1971, p. 28).

Type species. *Pangonia nana* Walker, 1850, Brazil, by original designation of Kröber (1930c).

Morphological Diagnosis. Length 8-12 mm. A distinct group defined by the antennal flagellum with an enlarged first flagellomere with a conspicuous dense tuft of hair, without obvious structural projections (Coscarón & Papavero 2009).

Species included. The subgenus includes three recognised species (Species List).

Distribution. South America. Predominantly occurring in the Amazon basin, including Ecuador, Brazil and Bolivia (Coscarón & Papavero 2009).

Tribe GONIOPSINI Lessard, tribe.n.

Type genus. *Goniops* Aldrich, 1982, by present designation (Figure 19).

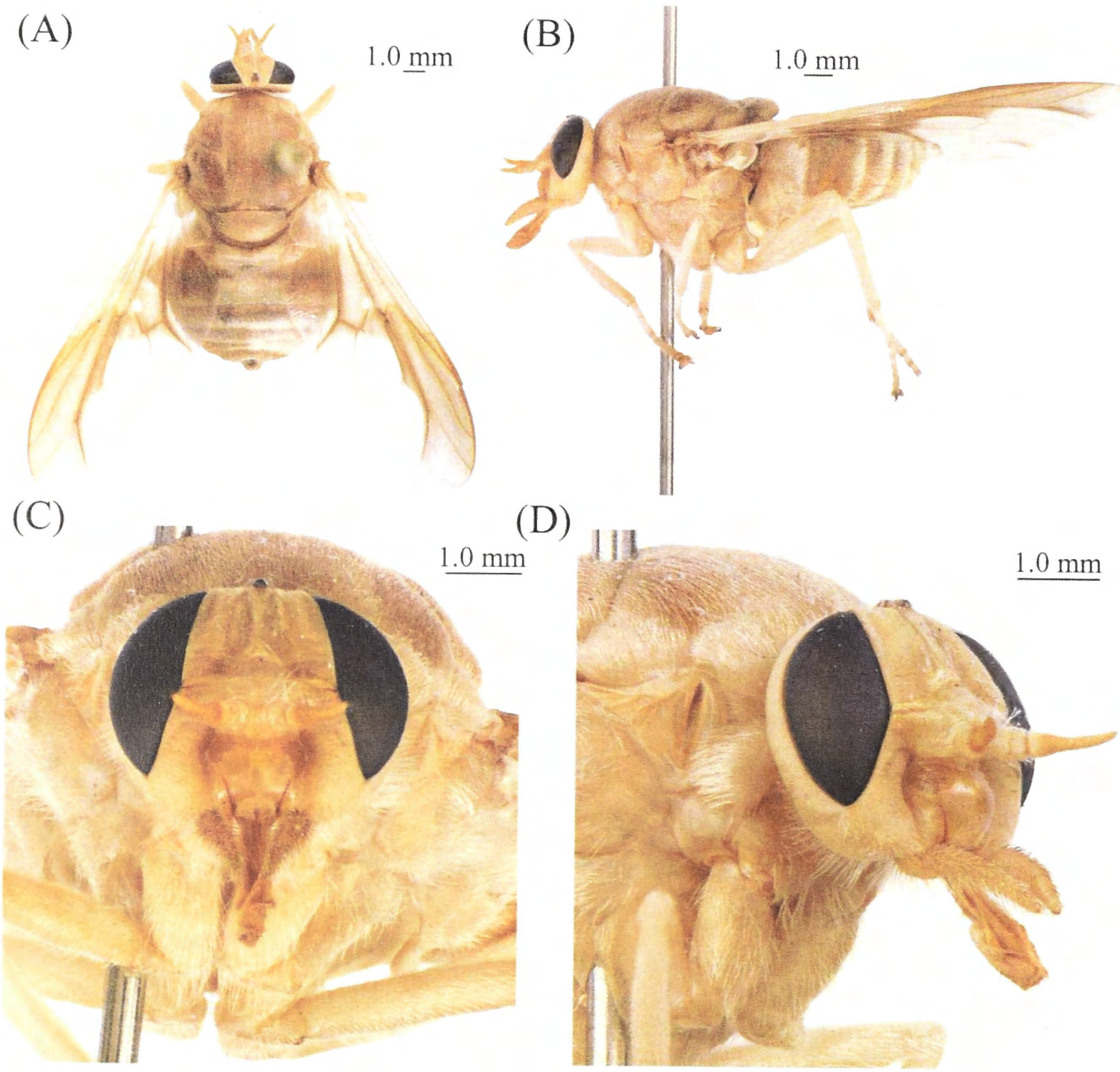

Figure 19: *Goniops* Aldrich, 1892, female of type species *Pangonia chrysocoma* Osten-Sacken, 1875: (a) dorsum; (b) side; (c) frons; (d) profile (ANIC).

Morphological diagnosis. A medium-size (12-14 mm), monotypic tribe represented by the single Nearctic species *Goniops chrysocoma* Osten-Sacken, 1875. Most similar to the Pangoniini and Philolichini, sharing the bare eyes and presence of a strong appendix on wing vein R_4. Eyes of the males holoptyic, and females possessing an extremely wide frons (index approaching 1.0) with a callus, face sunken, palpi without a definitive lateral bare concavity or apical pit, proboscis conspicuously reduced, and wings with a prominent brown radial staining (Figure 19). Both the male and female genitalia are similar to the Scionini, with the male hypopygium finger-like (Mackerras 1955, fig. 22, p. 483).

Distribution. Nearctic only. Restricted to the eastern coast of the United States of America.

Genus *GONIOPS* Aldrich, 1892 trans.n.

(Figure 19)

Goniops Aldrich, 1892, p. 236. Mackerras 1955, 1960. Monotypic for *Goniops hippoboscoides* Aldrich, 1982 (= *Pangonia chrysocoma* Osten-Sacken, 1875), USA, by original designation. Brennan (1935, p. 368); Mackerras (1955, p. 483); Stone (1930, p. 293).

Type species. Monotypic for *Goniops hippoboscoides* Aldrich, 1982 (= *Pangonia chrysocoma* Osten-Sacken, 1875; Figure 19), USA, by original designation.

Morphological diagnosis. A medium-size (12-14 mm), concolorous pale golden-brown monotypic genus with bare eyes, prominent, brown radially stained wings, distinguished from the Scionini by the small head, extremely wide frons with a prominent callus, sunken face, palpi without a definitive bare lateral concavity or apical pit, and conspicuously reduced proboscis (Figure 19).

Female. Length 12-14 mm. Ocelli present. Eyes bare. Head small, just over half the width of the scutum. Frons extremely wide, width usually greater than height (index 0.7 to 1.0), diverging, with a rudimentary callus, subcallus somewhat distinct, projecting and shining. Face extremely truncate, almost sunken near parafacials, shining. Antennal scape and pedicel small, equal to the width of the short and cylindrical flagellum, with eight distinct flagellomeres without projections. Palpi long, exceeding the length of the flagellum and equal to the length of the proboscis shaft, subcylindrical, tapering and hairy, without a lateral bare area or concavity, instead with a bare inner ridge. Proboscis extremely short, less than three quarters the head length, with large well-developed labella that are wider than the proboscis shaft. Scutum with at least traces of vittae. Abdomen short, wide and rotund, without distinct markings. Wings with pale brown radial staining; stigma inconspicuous; cells R_5 and M_3 open; vein R_4 curved to angulate, with strong appendix; M_1 vein without inflexion. Male and female genitalia without distinguishing features from remaining Scionini (Mackerras 1955).

Male. Smaller than females (length 10–12 mm). Eyes holoptic, with upper facets only slightly enlarged. Palpi more slender than females, cylindrical, hairy and without lateral concavity or apical pit.

Species included. The genus is represented by the type species only (Species List).

Distribution. Eastern United States of America, ranging from New York to Virgina, expanding westwards to Arkansas (Brennan 1935; Lessard *et al.* 2013; Mackerras 1955). Stone (1930) reported that the genus was also present in Florida but did not provide any further location data.

Biology. Adult females apparently do not feed on blood (Mackerras 1955) and are suspected nectar-feeders. Females have been witnessed depositing eggs on the underside of leaves and are watched over for several days before hatching, when the larvae fall to the ground and develop in the soil and plant debris (Mackerras 1955). According to Mackerras (1955), the larvae and pupa are morphologically similar to those of *Scaptia.*

Remarks. *Goniops* is hereby removed from the Scionini and placed within the novel tribe Goniopsini Lessard, **tribe.n.**, based on the distinct morphology of the genus, in addition to the well-supported monophyly of the monotypic species and strong genetic divergence from the Scionini and other tribes in the Pangoniinae (Figure 1).

Tribe MYCTEROMYIINI Coscarón & Philip, 1979

Morphological diagnosis. A valid description of the tribe was provided by Coscarón and Philip (1979, p. 429).

Genus *CAENOPANGONIA* Kröber, 1930 trans.n.

(Figure 20)

Caenopangonia Kröber, 1930b, p. 134. Type species *Diatomineura hirtipalpis* Bigot, 1892, Chile, by original designation. Coscarón & Philip (1979, p. 446); Coscarón & Papavero (1993, pp. 17, 60, 2009, pp. 9, 52).

Type species. *Diatomineura hirtipalpis* Bigot, 1892 (Figure 20), by original designation of Kröber (1930b).

Morphological diagnosis. Small to medium (length 9-14 mm) yellowish-brown species, with dichoptic eyes in both sexes, strong scutal vittae, spotting on the crossveins of the wing, conspicuously widened frons, and small, subcylindrical palpi with reduced apical

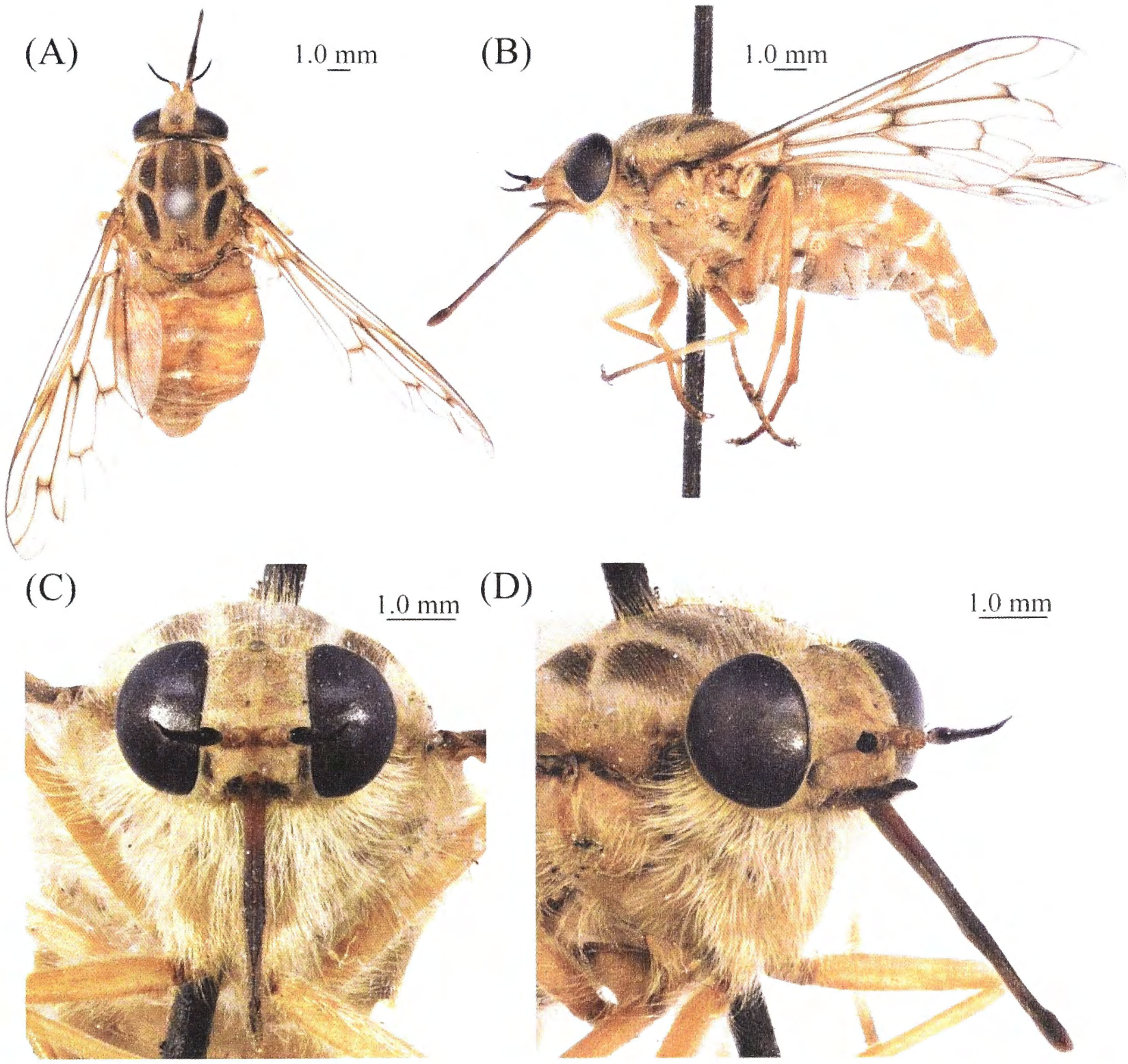

Figure 20: *Caenopangonia* Kröber, 1930, female of species *Mycteromyia brevirostris* Philippi, 1865: (a) dorsum; (b) side; (c) frons; (d) profile (SI).

pits (Figure 20). According to Coscarón and Philip (1979) this genus is distinguished from other members of the Mycteromyiini only by the less elongated thorax, wings and fore legs, and presence of the palps reduced apical pit.

Female. Length 11.5-14 mm. Eyes bare. Three distinct ocelli present. Frons extremely wide, width approximately equal to height (index 0.9), convex, diverging at dorsal and ventral margins, without obvious callus or transverse suture separating it from the subcallus. Face conspicuously truncate, almost sunken with a slight basal depression, without shine or obvious transverse suture to distinguish it from the bulging subcallus. Antennal scape and pedicel small, equal to the length of the tapering flagellum, divided into eight distinct flagellomeres without projections. Palpi small, approximately equal to

half the length of the flagellum and less than a quarter times the length of the proboscis shaft, cylindrical and rounded, with a reduced apical pit. Proboscis long, greater than one and a half times the length of the head, slender and chitonised, with small, weakly developed labella that are only slightly wider than the proboscis shaft. Scutum with conspicuous vittae exceeding the length of the transverse suture. Hind tibial spurs present. Abdomen elongated and narrowed, without distinct markings. Wings with clouds on crossveins; stigma inconspicuous; cell R_5 closed with petiole; cell M_3 open; vein M_1 without obvious inflexion; vein R_4 angulate, with an obvious appendix (Kröber 1930b; Coscarón & Philip 1979). Coscarón and Philip (1979) stated that the genitalia were similar to the Pangoniini, having boulbous distal spermathecal ampullae that were not chitonised, and distinctly wide caudal ducts of the spermathecae.

Male. Length 9-13 mm. Eyes dichoptic, with upper facets not enlarged. Palpi long, with first segment equal to or greater than the length of the second, cylindrical, without obvious apical pit or bare area. Genitalia were described by Coscarón and Philip (1979, p. 446) as having "flagella and aedeagus with round to elongate apodeme; dististyli subcylindrical, apically rounded or truncate in form of two small lobes".

Species included. A key to the three known species (Species List) was provided by Coscarón & Philip (1979, p. 450).

Distribution. South America. Predominantly Patagonian, ranging from the Ñuble to Osorno regions of Chile and the Neuquén region of Argentina (Coscarón & Philip 1979).

Biology. Nothing is known regarding the feeding and larval habits for the genus.

Remarks. *Caenopangonia* is hereby removed from the Scionini and reassigned to the more closely related tribe Mycteromyiini based on the distinct morphology of the genus. On an English translation of Kröber (1930b; deposited in the ANIC), Mackerras noted that *Caenopangonia* "reads like a *Mycteromyia* with a short proboscis" and therefore reduced *Caenopangonia* to a synonym of *Mycteromyia* Philippi, 1865 (Mackerras 1955, p. 483), which was accepted by Fairchild (1971, p. 12). Despite this, Coscarón and Philip (1979, p. 427) resurrected *Caenopangonia* and "questionably retained" the genus within the Scionini. Morphological exmaination reveals minor differences between *Caenopangonia* and the Mycteromyiini; Coscarón and Philip (1979, p. 450) stated the

Caenopangonia differed only in the "thorax, wings, and fore legs [being] not unusually elongated" like in the Mycteromyiini, which can be interpreted as typical intratribal variation among genera. In contrast, the differences between *Caenopangonia* and the Scionini are vastly greater, as *Caenopangonia* is distinguished by the dichoptic eyes in the male, females with extremely wide and densely haired frons appearing to merge with the subcallus due to the lack of a distinct transverse suture, as well as the sunken face, exceptionally strong scutal vittae, and elongated abdomen with rigid cuticle. Furthermore, the genitalia of *Caenopangonia* are more reminiscent of the Pangoniini, which were recovered as sister to the Mycteromyiini in the current molecular phylogenetic hypothesis for the Scionini (Lessard *et al.* 2013). Therefore, more extensive material of *Caenopangonia*, including the type species, is desired for future molecular studies.

DISCUSSION

The taxonomy and classification scheme for the austral horse fly tribe Scionini was successfully revised. This study facilitated the comprehensive redescription and validation of all genera, as more stable and robust concepts of genera were provided, especially for those that had historically suffered from poor taxonomic treatment. Several species previously belonging to the former subgenus *Scaptia* (*Pseudoscione*) were also reassigned to the newly revised genera of *Lepmia* (*L. atra, L. grisea, L. hibernus* and *L. leucothorax*) and *Parosca* (*Pr. albifrons, Pr. latipalpis* and *Pr. viridiventris*). Morphological examination also advocated the removal of the distinct genera *Caenopangonia* Kröber, 1930 **trans.n.** and *Goniops* Aldrich, 1892 **trans.n.** from the Scionini, which were formally reassigned to the more appropriate tribes Mycteromyiini and Goniopsini Lessard **tribe.n.**, respectively. The Scionini are now defined to include seventeen genera, including *Anzomyia* Lessard, **gen.n.**, *Aotearomyia* Lessard, **gen.n.**, *Apocampta* Schiner, 1867 **stat.n.**, *Copidapha* Enderlein, 1922 **stat.n.**, *Fidena* Walker, 1850, *Lepmia* Fairchild, 1969 **stat.n.**, *Myioscaptia* Mackerras, 1955 **stat.n.**, *Osca* Walker, 1850 **stat.n.**, *Palimmecomyia* Taylor, 1917 **stat.n.**, *Parosca* Enderlein, 1922 **stat.n.**, *Pityocera* Giglio-Tos, 1896, *Plinthina* Walker, 1850 **stat.n.**, *Pseudomelpia* Enderlein, 1922 **stat.n.**, *Pseudoscione* Lutz, 1918 **stat.n.**, *Scaptia* Walker, 1850, *Scione* Walker, 1850 and *Triclista* Enderlein, 1922 **stat.n.**

Future taxonomic studies would benefit from more extensive sampling of the South American genera, in particular *Fidena, Pityocera* and *Scione*, which possess strong morphological uniformity and outdated diagnostic keys that exclude multiple recently described and synonymised species. More genetic sampling of the genus *Lepmia* is also desired as the current phylogenetic hypothesis of the tribe includes only one specimen from a single species in the genus. Larval and pupal stages are unknown for the majority of genera of the Scionini and are only rudimentarily described for *Aotearomyia* Lessard, **gen.n.**, *Copidapha, Myioscaptia, Osca* and *Scaptia*. Although the limited availability of collected material has hindered the development of a thorough diagnosis of these stages, the immatures may provide a potential suite of putatively informative characters for future phylogenetic studies.

Species List: List of genera, subgenera and species of the austral horse fly tribe Scionini. Asterisks indicate specimens physically examined by author; dagger indicates type species. AU: Australia; CA: Central America; PNG: Papua New Guinea; SA: South America; USA: United States of America.

SCIONINI Enderlein, 1922

***Anzomyia* Lessard, 2012 (n=4)**
An. anomala (Mackerras, 1960) †* [AU]
An. chrysomallis Lessard, 2012* [AU]
An. herculensis Lessard, 2012* [NZ]
An. pegasus Lessard, 2012* [AU]

***Aotearomyia* Lessard, gen.n. (n=6)**
Ao. adrel (Walker, 1850) †* **trans.n.** [NZ]
Ao. brevipalpis (Kröber, 1931)* **trans.n.** [NZ]
Ao. lerda (Walker, 1850)* **trans.n.** [NZ]
Ao. montana (Hutton, 1901)* **trans.n.** [NZ]
Ao. milleri (Mackerras, 1957)* **trans.n.** [NZ]
Ao. ricardoae (Hutton, 1892)* **trans.n.** [NZ]

***Apocampta* Schiner, 1867 stat.n. (n=1)**
Ap. subcana (Walker, 1848) †* [AU]

***Copidapha* Enderlein, 1922 stat.n. (n=43)**
The *clavata* group
C. clavata (Macquart, 1838)* [AU]
C. orientalis (Mackerras, 1960)* [AU]
C. gemina (Walker, 1848)* [AU]

The *maculiventris* group:
The *maculiventris* subgroup
C. auripleura (Taylor, 1917)* [AU]
C. bicolorata (Taylor, 1918)* [AU]
C. calabyi (Mackerras, 1960)* [AU]
C. georgii (Taylor, 1918)* [AU]
C. guttipennis (Ferguson, 1924)* [AU]
C. maculiventris (Westwood, 1835)* [AU]
C. neotricolor (Taylor, 1918)* [AU]
C. occidentalis (Mackerras, 1960)* [AU]
C. regisgeorgii (Taylor, 1918)* [AU]
C. rufonigra (Ferguson, 1921)* [AU]
C. subappendiculata (Macquart, 1850)* [AU]
C. subcontigua (Ferguson, 1921)* [AU]
C. testaceomaculata (Macquart, 1850)* [AU]
C. xanthopilis (Ferguson, 1921)* [AU]
C. albibarba (Schuurmans & Stekhoven, 1926)* [PNG]
C. unilineata (Oldroyd, 1947) [PNG]

The *concolor* subgroup
C. aureohirta (Ricardo, 1900)* [AU]
C. baylessi (Lessard, 2012)* [AU]
C. casseli (Lessard, 2012)* [AU]
C. concolor (Walker, 1850)* [AU]
C. lasiophthalma (Macquart, 1834)* [AU]
C. moritae (Lessard, 2012)* [AU]
C. neoconcolor (Mackerras, 1960)* [AU]
C. quadrimacula (Walker, 1848)* [AU]
C. roei (Macleay, 1826) †* [AU]
C. turcatelae (Lessard, 2012)* [AU]
C. turneri (Lessard, 2012)* [AU]
C. wiegmanni (Lessard, 2012)* [AU]
C. auripilosa (Oldroyd, 1947)* [PNG]
C. bernhardi (Oldroyd, 1947) [PNG]
C. caliginosa (Walker, 1865)* [PNG]
C. flavibarbis (Oldroyd, 1949) [PNG]
C. floccosa (Oldroyd, 1947)* [PNG]

C. insularis (Oldroyd, 1947)* [PNG]
C. leonina (Oldroyd, 1947)* [PNG]
C. novaeguineensis (Ricardo, 1913) [PNG]
C. taylori (Oldroyd, 1947)* [PNG]

The *vicina* group
C. vicina (Taylor, 1918)* [AU]

Unplaced species
C. ianthina (White, 1915) [AU]
C. mackerrasi (Lessard, 2012)* [AU]

Fidena Walker, 1850 (n=99)

Subgenus *Fidena* Walker, 1850 (n=94)

F. (F.) abominata Philip, 1941 [SA]
F. (F.) adnaticornis Castro, 1945 [SA]
F. (F.) albibarba Enderlein, 1925* [CA, SA]
F. (F.) albitaeniata (Lutz, 1911) [SA]
F. (F.) analis (Fabricius, 1805) [SA]
F. (F.) atra Lutz & Castro, 1936 [SA]
F. (F.) atripes (Röder, 1886)* [SA]
F. (F.) aureopygia Kröber, 1931 [SA]
F. (F.) aureosericea Kröber, 1931 [SA]
F. (F.) auribarba (Enderlein, 1925) [CA, SA]
F. (F.) auricincta (Lutz & Neiva, 1909) [SA]
F. (F.) aurifasciata Enderlein, 1925 [SA]
F. (F.) aurimaculata (Macquart, 1838) [SA]
F. (F.) auripes (Ricardo, 1900)* [SA]
F. (F.) aurulenta Gorayeb, 1986 [SA]
F. (F.) basilaris (Wiedemann, 1828) [SA]
F. (F.) bicolor Kröber, 1930 [CA]
F. (F.) bistriga Fairchild & Rafael, 1985 [SA]
F. (F.) bocainensis (Lutz & Castro, 1936) [SA]
F. (F.) brachycephala Kröber, 1931* [SA]
F. (F.) brasiliensis Kröber, 1931 [SA]
F. (F.) brevistria (Lutz, 1909) [SA]
F. (F.) callipyga Castro, 1945 [SA]
F. (F.) campolarguense Azevedo de Bassi, 1997 [SA]
F. (F.) castanea (Perty, 1833)* [SA]
F. (F.) castaneiventris Kröber, 1934 [SA]
F. (F.) coscaróni Philip, 1969 [SA]
F. (F.) decipiens Kröber, 1931* [SA]
F. (F.) eriomera (Macquart, 1838) [SA]
F. (F.) eriomeroides (Lutz, 1909)* [CA, SA]
F. (F.) erythronotata (Bigot, 1892)* [SA]
F. (F.) fisheri Philip, 1978 [CA]
F. (F.) flavicrinis (Lutz, 1909)* [SA]
F. (F.) flavipennis Kröber, 1931* [CA, SA]
F. (F.) flavithorax (Kröber, 1930) [SA]
F. (F.) florisuga (Lutz, 1911) [SA]
F. (F.) foetterlei (Lutz, 1909) [SA]
F. (F.) freemani Barretto, 1957* [SA]
F. (F.) fulgifascies Barretto, 1957* [SA]
F. (F.) fulvithorax (Wiedemann, 1821) [SA]
F. (F.) fulvitibialis (Ricardo, 1900) [SA]
F. (F.) fumifera (Walker, 1854)* [SA]
F. (F.) fusca (Thunberg, 1827)* [SA]
F. (F.) griseithorax Burger, 2002 [CA]
F. (F.) haywardi Philip, 1967 [SA]
F. (F.) howardi Fairchild, 1941* [CA]
F. (F.) latifrons Kröber, 1930 [SA]
F. (F.) leonina Lutz, 1909* [SA]
F. (F.) leucopogon (Wiedemann, 1928) †* [SA]
F. (F.) lingens (Wiedemann, 1928) [SA]
F. (F.) lissorhina Gorayeb & Fairchild, 1987 [SA]
F. (F.) longipalpis Enderlein, 1925* [SA]
F. (F.) loricornis Kröber, 1931* [SA]
F. (F.) maculipennis Kröber, 1931 [SA]
F. (F.) marginalis (Wiedemann, 1830)* [SA]
F. (F.) mattogrossensis (Lutz, 1912)* [SA]
F. (F.) neglecta Kröber, 1931* [SA]
F. (F.) nigricans (Lutz, 1909)* [SA]
F. (F.) nigripennis (Guérin-Méneville, 1832) [SA]
F. (F.) nigripes (Röder, 1886)* [SA]
F. (F.) nigrivittata (Macquart, 1850) [SA]
F. (F.) nitens (Bigot, 1892)* [SA]
F. (F.) niveibarba Kröber, 1931 [SA]
F. (F.) nubiapex (Lutz, 1911) [SA]
F. (F.) obscuripes Kröber, 1931 [SA]
F. (F.) ochracea (Kröber, 1930)* [SA]
F. (F.) ochrapogon Wilkerson, 1979 [SA]
F. (F.) oldroydi (Barretto, 1957) [SA]
F. (F.) opaca (Brèthes, 1910)* [SA]
F. (F.) pallidula Kröber, 1933* [SA]
F. (F.) penicillata (Bigot, 1892)* [SA]
F. (F.) pessoai Barretto, 1957 [SA]
F. (F.) philipi Coscarón, 2001 [SA]
F. (F.) pseudoaurimaculata (Lutz, 1909)* [SA]
F. (F.) pubescens (Lutz, 1909)* [SA]
F. (F.) rhinophora (Bellardi, 1859)* [CA, SA]
F. (F.) rubrithorax Kröber, 1931 [SA]
F. (F.) rufibasis Kröber, 1931 [SA]
F. (F.) ruficornis (Kröber, 1931) [SA]
F. (F.) rufohirta (Walker, 1848)* [SA]
F. (F.) schildi (Hine, 1925)* [CA, SA]
F. (F.) silvatica Brèthes, 1920 [SA]
F. (F.) soledadei (Lutz, 1911) [SA]
F. (F.) sorbens (Wiedemann, 1828)* [SA]
F. (F.) splendens (Lutz, 1911) [SA]
F. (F.) submetallica (Brèthes, 1910) [SA]
F. (F.) sulfurea Wilkerson, 1979* [SA]
F. (F.) tenuistria (Walker, 1848) [SA]
F. (F.) trapidoi Fairchild, 1953* [CA]
F. (F.) trinidadensis Fairchild & Aitken, 1960* [SA]
F. (F.) vallensis Wilkerson, 1979 [SA]
F. (F.) venosa (Wiedemann, 1821) [SA]
F. (F.) winthemi (Wiedemann, 1819)* [SA]
F. (F.) zonalis Kröber, 1931* [SA]

Subgenus *Laphriomyia* Lutz, 1911 (n=3)

F. (La.) kroeberi Kröber, 1931 [SA]
F. (La.) mirabilis Lutz, 1911† [SA]
F. (La.) palidetarsis Kröber, 1930 [SA]

Subgenus *Leptofidena* Kröber, 1930 (n=1)

F. (Lf.) morio (Wulp, 1881) †* [SA]

Subgenus *Neopangonia* Lutz, 1909 (n=1)
F. (Ne.) pusilla (Lutz, 1909) † [SA]

Lepmia Fairchild, 1969 stat.n. (n=6)
L. atra (Philippi, 1865)* **trans.n.** [SA]
L. grisea (Jaennicke, 1867)* **trans.n.** [SA]
L. hibernus (Wilkerson & Coscarón, 1984)* **trans.n.** [SA]
L. leucothorax (Ricardo, 1900)* **trans.n.** [SA]
L. molesta (Wiedemann, 1828) †* [SA]
L. seminigra (Ricardo, 1902)* [SA]

Myioscaptia Mackerras, 1955 stat.n. (n=11)
M. calliphora Mackerras, 1960* [AU]
M. collessi Lessard, 2013* [AU]
M. bancrofti (Austen, 1912)* [AU]
M. gibbula (Walker, 1848)* [AU]
M. inopinata Fairchild & Mackerras, 1977* [AU]
M. lambkinae Lessard, 2013* [AU]
M. muscula (English, 1955)* [AU]
M. ferromontana Daniels 2011* [AU]
M. nigroapicalis Mackerras, 1960* [AU]
M. nigrocincta Mackerras, 1960* [AU]
M. violacea (Macquart, 1850) †* [AU]

Osca Walker, 1850 stat.n. (n=11)
O. abdominosa (Philip, 1969) [SA]
O. albithorax (Macquart, 1838) [SA]
O. aureonigra Kröber, 1931* [SA]
O. aureopygia (Philip, 1969) [SA]
O. collaris (Philippi, 1865) [SA]
O. lata (Guèrin-Méneville, 1835) †* [SA]
O. rubriventris Kröber, 1930* [SA]
O. rufa (Macquart, 1838)* [SA]
O. sublata (Philip, 1969) [SA]
O. varia (Walker, 1848)* [SA]
O. nigribella (Wilkerson, 1984) [SA]

Palimmecomyia Taylor, 1917 stat.n. (n=2)
Pa. walkeri (Newman, 1857) †* [AU]
Pa. pictipennis Mackerras, 1960* [AU]

Parosca Enderlein, 1922 stat.n. (n=3)
Pr. albifrons (Macquart, 1938)* **trans.n.** [SA]
Pr. latipalpis (Macquart, 1849)* **trans.n.** [SA]
Pr. viridiventris (Macquart, 1838) †* [SA]

Pityocera Giglio-Tos, 1896 (n=5)
Subgenus *Elaphella* Bezzi, 1913 (n=1)
Pt. (El.) cervus (Wiedemann, 1828) †* [SA]

Subgenus *Pityocera* Giglio-Tos, 1896 (n=1)
Pt. (Pt.) festae Giglio-Tos, 1896†* [SA]

Subgenus *Pseudelaphella* Kröber, 1930 (n=3)
Pt. (Pe.) nana (Walker, 1850) †* [SA]
Pt. (Pe.) nigribasis Fairchild, 1964 [?]
Pt. (Pe.) patellicornis Kröber, 1930* [SA]

Plinthina Walker, 1850 stat.n. (n=12)
Pl. arnhemensis Lessard, 2011* [AU]
Pl. aurifulga Lessard, 2011* [AU]
Pl. beyonceae Lessard, 2011* [AU]
Pl. binotata (Latreille, 1812) †* [AU]
Pl. clelandi (Ferguson, 1921)* [AU]
Pl. cinerea (Ricardo, 1915)* [AU]
Pl. divisa (Walker, 1850)* [AU]
Pl. nelsonae Lessard, 2011* [AU]
Pl. nigerrima Mackerras, 1960* [AU]
Pl. nigripuncta Lessard, 2011* [AU]
Pl. subcinerea Mackerras, 1960* [AU]
Pl. vertebrata (Bigot, 1892)* [AU]

Pseudomelpia Enderlein, 1922 stat.n. (n=1)
Pm. horrens Enderlein, 1925†* [SA]

Pseudoscione Lutz, 1918 stat.n. (n=9)
Ps. australis (Philippi, 1865)* [SA]
Ps. dorsoguttata (Macquart, 1850)* [SA]
Ps. fenestrata (Macquart, 1846) [SA]
Ps. flavipes (Enderlein, 1929) [SA]
Ps. longipennis (Ricardo, 1902) †* [SA]
Ps. stictica Wilkerson & Coscarón, 1984* [SA]
Ps. subandina (Philippi, 1865)* [SA]
Ps. subulipalpis (Enderlein, 1929) [SA]
Ps. vittata (Philippi, 1865)* [SA]

Scaptia Walker, 1850 (n=26)
S. abdominalis (Ricardo, 1917)* [AU]
S. alpina alpina Mackerras, 1960* [AU]
S. alpina hardyi Mackerras, 1960* [AU]
S. aurata (Macquart, 1838) †* [AU]
S. auranticula Mackerras, 1960* [AU]
S. aureovestita (Ferguson & Henry, 1920)* [AU]
S. auriflua (Donovan, 1805)* [AU]
S. aurinigra Lessard, 2013* [AU]
S. aurinotum Mackerras, 1960* [AU]
S. barbara Mackerras, 1960* [AU]
S. berylensis (Ricardo, 1915)* [AU]
S. brevirostris (Macquart, 1850)* [AU]
S. fulgida (Ferguson & Henry, 1920)* [AU]
S. jacksoniensis (Guérin, 1831)* [AU]
S. jacksonii (Macquart, 1838)* [AU]
S. limbithorax (Macquart, 1855)* [AU]
S. minuscula Mackerras, 1960* [AU]
S. monticola Mackerras, 1960* [AU]
S. norrisi Mackerras, 1960* [AU]
S. orba Mackerras, 1960* [AU]
S. patula (Walker, 1848)* [AU]
S. plana (Walker, 1848)* [AU]
S. pulchra (Ricardo, 1915)* [AU]

S. similis Mackerras, 1960* [AU]
S. testacea (Macquart, 1838)* [AU]
S. tricolor (Walker, 1848)* [AU]

Scione Walker, 1850 (n=41)

Sc. ablusus Fairchild, 1964 [CA]
Sc. acer Philip, 1958 [SA]
Sc. albifasciata (Macquart, 1846)* [SA]
Sc. albohirta Kröber, 1930 [SA]
Sc. albopilosus Burger, 2002 [CA]
Sc. aurulans (Wiedemann, 1830)* [CA, SA]
Sc. bilineata Philip, 1967 [SA]
Sc. brevibeccus Wilkerson, 1979* [SA]
Sc. brevistriga Enderlein, 1925* [SA]
Sc. cingulata (Enderlein, 1925) [SA]
Sc. claripennis Ricardo, 1900 [SA]
Sc. costaricana Szilády, 1926* [CA]
Sc. crassa Szilády, 1926 [SA]
Sc. cupreus Wilkerson, 1979 [SA]
Sc. distincta (Schiner, 1868)* [SA]
Sc. equatoriensis Surcouf, 1919* [SA]
Sc. equivexans Wilkerson, 1979 [SA]
Sc. flavescens (Enderlein, 1930) [SA]
Sc. flavohirta Ricardo, 1902* [SA]
Sc. fulva Ricardo, 1902* [SA]
Sc. fumipennis Kröber, 1930 [SA]
Sc. fusca Ricardo, 1902* [SA]
Sc. grandis Philip, 1943 [SA]
Sc. huancabambae Kröber, 1930* [SA]
Sc. immaculata (Kröber, 1930) [SA]
Sc. incompleta (Macquart, 1846) †* [SA]
Sc. limbativena Enderlein, 1925 [SA]
Sc. longirostris Brèthes, 1920 [SA]
Sc. maculipennis (Schiner, 1868)* [SA]
Sc. minor (Macquart, 1847)* [SA]
Sc. minuta Szilády, 1926 [SA]
Sc. nigripes (Kröber, 1930) [SA]
Sc. obscurefemorata Kröber, 1930 [SA]
Sc. picta Szilády, 1926 [SA]
Sc. punctata Szilády, 1926 [SA]
Sc. rhinothrix Wilkerson, 1979 [SA]
Sc. rufescens (Ricardo, 1900)* [SA]
Sc. rufipes (Kröber, 1930)* [SA]
Sc. serratus Wilkerson, 1979 [SA]
Sc. strigata (Enderlein, 1925) [SA]
Sc. youngi Wilkerson, 1979 [SA]

Triclista Enderlein, 1922 stat.n. (n=3)

T. guttata (Donovan, 1805)* [AU]
T. media (Walker, 1848)* [AU]
T. singularis (Macquart, 1846) †* [AU]

GONIOPSINI Lessard, tribe.n.

Goniops Aldrich, 1892 trans.n. (n=1)

G. chrysocoma Aldrich, 1892 †* [USA]

MYCTEROMYIINI Coscarón & Philip, 1979

Caenopangonia Kröber, 1930 trans.n. (n=3)

Cn. asper (Philip, 1958) [SA]
Cn. brevirostris (Philippi, 1865)* [SA]
Cn. hirtipalpis (Bigot, 1892) † [SA]

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Chapter Nine

9. General Conclusions

This study updated the species-level taxonomy for the Australian Scionini that has not been revised in over 50 years. Traditional morphological characters were useful in delimiting and describing 18 novel species from several genera that have accumulated in museum collections since Mackerras' (1960) previous work, including the novel genus *Anzomyia* Lessard, 2012 (Chapters Three to Six). In addition, the first quantitative phylogenetic hypothesis for the Scionini was provided using contemporary molecular methods (Chapter Seven). Multiple genetic markers, including mitochondrial and nuclear genes were valuable in resolving the phylogenetic relationships of a taxonomically difficult group, despite limited traditional morphology-based classification schemes. In the large molecular analysis, the monophyly of the Scionini and its individual genera were

well-supported, excluding the widespread genus *Scaptia,* which was identified as strongly paraphyletic and subsequently amended in the larger taxonomic revision of the Scionini (Chapter Eight). A novel diagnostic key to the genera of the Scionini was also developed to benefit future workers. Divergence time estimation indicated that the Scionini most likely originated in Australia, and that a complex process of both vicariance and long distance dispersal shaped the current biogeography of the tribe (Chapter Seven). The Scionini are now defined to include over 280 species from 17 recognised genera, including *Anzomyia* Lessard, 2012, *Aotearomyia* Lessard, 2014, *Apocampta* Schiner, 1867, *Copidapha* Enderlein, 1922, *Fidena* Walker, 1850, *Lepmia* Fairchild, 1969, *Myioscaptia* Mackerras, 1955, *Osca* Walker, 1850, *Palimmecomyia* Taylor, 1917, *Parosca* Enderlein, 1922, *Pityocera* Giglio-Tos, 1896, *Plinthina* Walker, 1850, *Pseudomelpia* Enderlein, 1922, *Pseudoscione* Lutz, 1918, *Scaptia* Walker, 1850, *Scione* Walker, 1850 and *Triclista* Enderlein, 1922.

9.1 Stationary genera of the Scionini

Multiple mitochondrial (COI and COII) and nuclear (AATS, CAD and 28S) genes were successful in providing the first quantitative phylogenetic hypothesis for the Scionini (Chapter Seven; Figure 7.2). The selected genes were straightforward to amplify and sequence, facilitating the identification of specimens distributed widely throughout the Southern Hemisphere. Molecular data also supported the monophyly of the Tabanidae subfamilies, reinforcing the previous molecular studies of Wiegmann *et al.* (2000) and Morita (2008). Moreover, the inclusion of the Scionini in the molecular analysis confirmed the placement of the tribe within a well-supported monophyletic Pangoniinae.

The genera *Fidena, Pityocera* and *Scione* were all individually recovered as well-supported monophyletic clades (Chapter Seven; Figure 7.2). The molecular data also confirmed the placement of *Pityocera* within the Scionini, instead of belonging to a separate tribe as previously proposed by Kröber (1932). Furthermore, the molecular monophyly of those genera agreed with traditional morphology-based classification schemes in the larger taxonomic revision of the Scionini (Chapter Eight). Based on the consistent morphological and molecular evidence, *Fidena, Pityocera* and *Scione* were accepted as valid genera of the Scionini.

9.2 Revised genera of the Scionini

The genus *Scaptia,* in its unrevised form, was identified as radically paraphyletic in the phylogenetic hypothesis of the Scionini, indicating that major taxonomic revision was warranted (Chapter Seven; Figure 7.2). This paraphyly corresponded to several well-supported monophyletic clades corresponding to the former subgenera of *Scaptia* and other erroneously synonymised genera. *Scaptia* was revised in the large taxonomic revision of the Scionini, which facilitated the raising of several of the former subgenera to genus level (*Lepmia* and *Myioscaptia*), in addition to reinstating genera that were previously reduced to subgenera of *Scaptia* (*Palimmecomyia, Plinthina, Pseudomelpia* and *Pseudoscione*) and resurrecting several incorrectly synonymised genera (*Apocampta, Copidapha, Parosca, Osca* and *Triclista*).

9.2.1 Genus Scaptia *Walker, 1850*

The Australian genus *Scaptia* was first introduced by Walker (1850), although the type species *Pangonia aurata* Macquart, 1838 was designated sometime later by Coquillett (1910). Many workers broadly applied this genus to the majority of Australian, New Zealand and South American species of Scionini by continuing to implement the previous subgenera of *Scaptia* and accepting the incorrect synonymy of *Osca* (Coscarón and Wilkerson 1985; Coscarón and Gonzalez 2001; Coscarón and Iide 2003; Daniels 1989; Fairchild 1956, 1966a, 1969, 1971; Fairchild and Burger 1994; Ferguson 1924, 1926; Mackerras 1955, 1957, 1960, 1961, 1964; Oldroyd 1947; Philip 1967; Wilkerson 1984; Wilkerson and Coscarón 1984).

In the current phylogenetic hypothesis for the Scionini, the type species *aurata* formed a well-supported monophyletic clade with the remainder of the Australian species from the former subgenus *Scaptia* (*Scaptia*) (Chapter Seven; Figure 7.2). Moreover, *Scaptia* was genetically distinct from the remaining genera of the Scionini and recovered as sister to *Fidena* + *Pityocera*. Morphological examination confirmed that *Scaptia* was a unique taxon of the Scionini, distinguished by the parallel frons of females, with large pointed and sabre-like palpi, a short thick proboscis with large well-developed labella, rather stout and rotund abdomen that is not obviously dorsoventrally compressed and wings with cells R_5 and M_3 open (Chapter Eight). The molecular data and morphology were used to

redefine *Scaptia* as pertaining to the type species *aurata* and the Australian species from the former subgenus *Scaptia* (*Scaptia*). The results also facilitated the resurrection of *Apocampta, Osca* and *Triclista*, which were previously reduced to synonymies of *Scaptia* (Ferguson 1924, 1926), as they formed distinct monophyletic clades in the phylogenetic analysis. With the description of the novel species *Scaptia aurinigra* Lessard, 2013 (Chapter Six), *Scaptia* now contains 26 recognised species endemic to Australia.

9.2.2 Genus Triclista *Enderlein, 1922*

Triclista was first introduced by Enderlein (1922) who merely listed the type species *Pangonia singularis* Macquart, 1846 (under the synonym *Pangonia limbinevris* Macquart, 1855) in a rudimentary key to the genera of the Scionini. The genus was not formerly described until three years later (Enderlein 1925), however, Ferguson (1926) reduced *Triclista* as a synonym of *Scaptia* based on modest morphological differences, and the synonymy was adopted by subsequent authors (Daniels 1989; Mackerras 1955, 1960). Molecular results confirmed the well-supported monophyly of *Triclista,* including the type species *singularis* (Chapter Seven; Figure 7.2). In addition, *Triclista* was firmly separated and recovered as sister to the larger clade containing *Scaptia* and the majority of South American genera. Morphology also supported the distinct separation of *Triclista* from *Scaptia*, distinguished by the larger size, clouded wings with closure of cells R_5 and M_3 and obvious white markings of the abdomen (Chapter Eight). Therefore, *Triclista* was formally resurrected to a valid genus of the Scionini, based on the molecular data and distinct morphology of the genus.

9.2.3 Genus Apocampta *Schiner, 1867*

Apocampta was first introduced by Schiner (1867, 1868) as a monotypic genus of the Pangoniinae and designated with the type species *Chrysops subcana* Walker, 1848 (under the synonym *Apocampta nigra* Schiner, 1868). This was adopted by Enderlein (1922, 1925), although the genus was reduced to a synonym of *Scaptia* by Ferguson (1926), which was accepted by subsequent workers (Daniels 1989; Mackerras 1955, 1960). The phylogenetic analysis indicated that *Apocampta* was a well-supported and genetically distinct clade formed of multiple specimens of the type species *subcana* (Chapter Seven;

Figure 7.2). Furthermore, *Apocampta* was firmly separated from the genus *Scaptia* and recovered as sister to *Osca*. Morphology also supported the separation of *Apocampta* from *Scaptia*, distinguished by the smaller size, narrow to oblong abdomen and dark, radially stained wings (Chapter Eight). Therefore, *Apocampta* was formally resurrected to a valid genus of Scionini.

9.2.4 Genus Osca *Walker, 1850*

Walker (1850) originally presented *Osca* as a genus of the Tabanidae, which was eventually designated with the type species *Tabanus lata* Guèrin-Méneville, 1835 by Coquillett (1910). Conversely, Ferguson (1924) reduced *Osca* to a synonymy of *Scaptia*, which was accepted by successive authors (Cárdenas *et al.* 2009; Chainey *et al.* 1994; Coscarón and Papavero 1993, 2009; Coscarón and Wilkerson 1985; Fairchild 1956, 1966b; Mackerras 1955, 1960; Philip 1967; Wilkerson 1984; Wilkerson and Fairchild 1984). Interestingly, Kröber (1930b, 1932, 1934) challenged the synonymy of *Osca* and continued to apply the name to the South American species. Molecular results indicated the well-supported genetic distinctiveness of *Osca,* which was formed of multiple specimens of the type species *lata* (Chapter Seven; Figure 7.2). Moreover, *Osca* was firmly separated from *Scaptia* and instead recovered as sister to *Apocampta*. Morphology further supported the separation of *Osca* from *Scaptia,* distinguished by the bumblebee-like appearance, and oblong, dorsocentrally compressed abdomen with an obvious lateral fringe of dense hair (Chapter Eight). Therefore, *Osca* was formally resurrected to a valid genus of the Scionini.

9.2.5 Genus Pseudoscione *Lutz, 1918*

Lutz in Lutz, Araujo, and Fonseca (1918) originally presented *Pseudoscione* in a species checklist without a formal description, designation of type species or any statement indicating that the genus was new. Fairchild (1950) formally designated the type species *Diatomineura longipennis* Ricardo, 1902 sometime later. The first description of the taxon was provided by Mackerras (1955), who also reduced *Pseudoscione* to a subgenus of *Scaptia*. This synonymy was accepted by most authors who continued to broadly apply *Scaptia* (*Pseudoscione*) to the majority of Australian, New Zealand and South American

species of Scionini (Coscarón and Papavero 1993, 2009; Fairchild 1969; Mackerras 1955, 1957, 1960, 1964; Wilkerson and Coscarón 1984; Wilkerson and Fairchild 1984).

The phylogenetic analysis identified the former subgenus *Scaptia* (*Pseudoscione*) as strongly paraphyletic (Chapter Seven; Figure 7.2), comprising four individually monophyletic clades corresponding to *Pseudoscione sensu stricto* (the clade containing *vitatta* Philippi, 1865 + *australis* Philippi, 1865 + *dorsoguttata* Macquart, 1850, South America), *Copidapha* and *Parosca*, which were previously synonymised (Ferguson 1926; Mackerras 1955), and the novel New Zealand genus *Aotearomyia*. These four clades were formally revised as separate genera in the taxonomic revision of the Scionini (Chapter Eight). Morphology also confirmed that *Pseudoscione* was a distinct taxon of the Scionini, distinguished by the short and thick palpi with a prominent deep lateral bare concavity, and proboscis with reduced labella equal to the width of the proboscis shaft, and separated from *Scione* by the open wing cell M_3 (Chapters Five and Eight). Moreover, *Pseudoscione* was firmly separated from its sister *Parosca* in the phylogenetic analysis (Chapter Seven; Figure 7.2). Therefore, based on the distinct morphology and molecular evidence, *Pseudoscione* was reinstated to a valid genus within the Scionini.

9.2.6 Genus Parosca *Enderlein, 1922*

Enderlein (1922) first introduced *Parosca* without any formal diagnosis by simply including the type species *Pangonia viridiventris* Macquart, 1838 in a taxonomic key to the now synonymised subfamily Melpiinae. Eventually, the genus was formally described by Enderlein (1925). The taxonomy of the genus has been historically unclear, as Kröber (1932) stated that *Parosca* was ill-defined and included an excessive number of heterogeneous species. Furthermore, workers were unable to agree upon which species to include in the genus (Enderlein 1925; Kröber 1930b). *Parosca* was at one time reduced to a synonym of *Listrapha* Enderlein, 1922 by Kröber (1934), however, this synonymy was found to be incorrect (Chapter 8) since *Listrapha* was first reduced to a synonym of *Parosca* sometime earlier by Kröber (1930). Therefore, *Parosca* has page priority even though both genera were described at the same time (Enderlein 1922). Both genera were eventually reduced to synonyms of *Scaptia* (*Pseudoscione*) by Mackerras (1955).

Molecular results confirmed the well-supported monophyly of *Parosca,* including the type species *viridiventris* (Chapter Seven; Figure 7.2). Furthermore, *Parosca* was genetically distinct from the remainder of the Scionini and recovered as sister to *Pseudoscione*. Morphology also confirmed that *Parosca* was a unique genus of Scionini, distinguished from *Pseudoscione* by the broad build, proboscis with slightly thicker labella, and the more extensively flattened, broad, triangular, long and dorsally rotated palpi. Therefore, *Parosca* was formally resurrected to a valid genus of Scionini. Morphological examination also facilitated the transfer of *Parosca albifrons* (Macquart, 1938), *Parosca latipalpis* (Macquart, 1849) and the type species *Pr. viridiventris* from their previous position within the former subgenus *Scaptia* (*Pseudoscione*), based on the distinct form of the flat, broad and triangular palpi, as initially suggested by Kröber (1930b). A novel taxonomic key to species was also developed to accommodate the revised species included in the genus.

9.2.7 Genus Copidapha *Enderlein, 1922*

Enderlein (1922) originally presented *Copidapha* without any official diagnosis by simply listing the type species *Pangonia roei* Macleay, 1826 (under synonym *Copidapha bifasciata* Enderlein, 1925) in a rudimentary taxonomic key to the now synonymised subfamily Melpiinae. *Copidapha* was formally described sometime after by Enderlein (1925), however, the genus was reduced to synonym of *Scaptia* by Ferguson (1926) and collapsed under the former subgenus *Scaptia* (*Pseudoscione*) by Mackerras (1955). This synonymy was adopted in the proceeding work of others (Daniels 1989; Mackerras 1960, 1964).

Molecular results confirmed the well-supported monophyly of *Copidapha*, including the type species *roei* and the Australian members of the former subgenus *Scaptia* (*Pseudoscione*) (Chapter Seven; Figure 7.2). Moreover, *Copidapha* was firmly separated from *Pseudoscione* and recovered as an individual clade sister to all Scionini, excluding *Anzomyia* and *Aotearomyia*. Morphology also confirmed that *Copidapha* was a distinct member of the Scionini, distinguished from *Pseudoscione* by the truncate to moderately bulging face, wide palpi, and labella that are only somewhat wider than the proboscis shaft (Chapters Five and Eight). Based on the morphology and molecular evidence, *Copidapha* was formally resurrected. Mackerras (1955) alluded to the separation of

Copidapha from the former subgenus *Scaptia* (*Pseudoscione*) by indicating that the name *Copidapha* would become available if the Australian members ever needed to be differentiated from the remaining species. This was demonstrated in Chapter Five (Figure 5.1), displaying the morphological discrepancies in the head structure of the regional *Aotearomyia* (referred to as New Zealand members), *Copidapha* (Australian) and *Pseudoscione* (South American) genera. Therefore, *Copidapha* is now a valid genus of the Scionini.

Seven novel species were also identified, named and described in *Copidapha* (Chapter Five), originally treated as the former subgenus *Scaptia* (*Pseudoscione*) before the genus was formally revised (Chapters Seven and Eight). The new species included *Copidapha baylessi* Lessard, 2012, *Copidapha casseli* Lessard, 2012, *Copidapha mackerrasi* Lessard, 2012, *Copidapha moritae* Lessard, 2012, *Copidapha turcatelae* Lessard, 2012, *Copidapha turneri* Lessard, 2012, and *Copidapha wiegmanni* Lessard, 2012. The genus *Copidapha* now comprises 44 recognised species from Australia and New Guinea, and the new species were included in an updated diagnostic key to species.

9.2.8 Genus Palimmecomyia *Taylor, 1917*

Taylor (1917) first described *Palimmecomyia* as a monotypic genus and designated the type species *Pangonia walkeri* Newman, 1857 (under the synonym *Palimmecomyia celaenospila* Taylor, 1917), as adopted by Ferguson (1926). Based on the structural similarities of the frons, proboscis and palpi, Mackerras (1955, 1960) reduced *Palimmecomyia* as a subgenus of *Scaptia*, as well as describing an additional species *Palimmecomyia pictipennis* Mackerras, 1960. Although absent in the molecular analysis, morphological examination suggested that *Palimmecomyia* was a unique genus of the Scionini and was identified as being most closely related to *Copidapha*, but distinguished by the peculiar shining wax-like cuticle, orange wings with striking brown staining at tips, and abdomen with distinct brown markings at the medial and lateral margins (Chapter Eight). Therefore, *Palimmecomyia* was reinstated to a valid genus of the Scionini.

9.2.9 Genus Myioscaptia *Mackerras, 1955*

In one of the largest revisions of the Pangoniinae, Mackerras (1955) introduced *Myioscaptia* as a subgenus of *Scaptia* and designated the type species *Pangonia violacea* Macquart, 1850, which was adopted by others (Daniels 1989; Fairchild and Mackerras 1977; Mackerras 1960). Molecular results confirmed the well-supported monophyly of *Myioscaptia,* including the type species *violacea* (Chapter Seven; Figure 7.2). Moreover, *Myioscaptia* was firmly separated from the remaining Scionini and recovered as sister to *Plinthina*. Morphology also supported the molecular results, revealing that *Myioscaptia* was a unique genus distinguished from other genera by the smaller rotund size, with short rounded and leaf-like palpi and less obvious scutal and abdominal markings compared to *Plinthina* (Chapters Six and Eight). Therefore, *Myioscaptia* was taxonomically raised from its previous position as a subgenus and is now a valid genus of the Scionini.

Two novel species were also identified, named and described in *Myioscaptia* (Chapter Six), originally treated as the previous subgenus *Scaptia* (*Myioscaptia*) before the genus was formally revised (Chapters Seven and Eight). Furthermore, the taxonomic key to species was updated to include all eleven known species of the genus, including the novel taxa, *Myioscaptia collessi* Lessard, 2013 and *Myioscaptia lambkinae* Lessard, 2013, and *Myioscaptia inopinata* Fairchild and Mackerras, 1977 that was described after the work of Mackerras (1960).

9.2.10 Genus Plinthina *Walker, 1850*

Walker (1850) originally presented *Plinthina* as a monotypic genus and designated the type species *Pangonia binotata* Latreille, 1812 (under the synonym *Pangonia macroporum* Macquart, 1838). Ferguson (1926) was the first to recognise *Plinthina* as a subgenus of *Scaptia*, which was adopted by Mackerras (1955, 1960) and Daniels (1989). The molecular analysis demonstrated the well-supported monophyly of *Plinthina*, including the type species *binotata* (Chapter Seven; Figure 7.2). In addition, *Plinthina* was considerably divergent from the remaining genera of the Scionini and recovered as sister to *Myioscaptia*. Morphology supported *Plinthina* as a unique taxon of the Scionini, distinguished from other members by the distinct marbling of the wings, although sometimes rather subtle, short thick, broad and flattened palpi and distinct markings on

the scutum and abdomen (Chapters Three and Eight). Therefore, *Plinthina* was formally reinstated to a valid genus of the Scionini

Five novel species were also identified, named and described in *Plinthina* (Chapter Three), originally treated as the former subgenus *Scaptia* (*Plinthina*) before the tribe was formally revised (Chapters Seven and Eight). These new species include *Plinthina arnhemensis* Lessard, 2011, *Plinthina aurifulga* Lessard, 2011, *Plinthina beyonceae* Lessard, 2011, *Plinthina nelsonae* Lessard, 2011 and *Plinthina nigripuncta* Lessard, 2011. These new species effectively doubled the known size of the genus and were included in a revised taxonomic key to species (Chapter Three).

9.2.11 Genus Pseudomelpia *Enderlein, 1922*

Enderlein (1922) introduced *Pseudomelpia* as a monotypic genus and designated the type species *Pseudomelpia horrens* Enderlein, 1925 (described later in Enderlein 1925) in a taxonomic key to the former tribe Silviini. *Pseudomelpia* was only formally described sometime later by Kröber (1930b) and was accepted as a genus by Fairchild (1966a). Despite this, Mackerras (1955) reduced *Pseudomelpia* to a subgenus of *Scaptia,* which has since been adopted by most authors (Fairchild 1969; Fairchild and Burger 1994; Coscarón and González 2001; Coscarón and Papavero 1993, 2009).

Although absent in the molecular analysis, morphological examination confirmed that *Pseudomelpia* was a unique taxon of Scionini (Chapter Eight). Moreover, *Pseudomelpia* was identified as being closely related to *Anzomyia* (Chapters Four and Eight), but distinguished by the extremely short and thick proboscis, basal four antennal flagellomeres appearing as fused, and with short swollen club-like palpi. Therefore, *Pseudomelpia* was formally reinstated to a valid genus of the Scionini.

9.2.12 Genus Lepmia *Fairchild, 1969*

Fairchild (1969) first described *Lepmia* as a subgenus of *Scaptia* and designated the type species *Pangonia molesta* Wiedemann, 1828. Many workers have since continued to treat *Lepmia* as a subgenus of *Scaptia* (Coscarón and Iide 2003; Coscarón and Papavero 1993,

2009; Fairchild 1971; Fairchild and Burger 1994). Morphological examination identified *Lepmia* as a unique taxon (Chapter Eight) and can be distinguished by the densely haired scutum, large bulbous abdomen, moderately sized and thick proboscis with small reduced labella, and more bulging and less projecting face, and palpi that are usually short, broad, flat and blunt, with an extensive bare area. Taxonomic revision of the Scionini also facilitated the transfer of *Lepmia atra* (Philippi, 1865), *Lepmia grisea* (Jaennicke, 1867), *Lepmia hibernus* (Wilkerson and Coscarón, 1984) and *Lepmia leucothorax* (Ricardo, 1900) from the species previous position within the former subgenus *Scaptia* (*Pseudoscione*) (Chapter Eight), and a novel diagnostic key was developed to accommodate the revised species of the genus. Molecular results demonstrated the firm separation of *Lepmia*, represented by *L. leucothorax*, from the remainder of the Scionini and recovered as sister to the clade containing *Scione* + *Parosca* + *Pseudoscione* (Chapter Seven; Figure 7.2). Therefore, based on the distinct morphology and molecular evidence, *Lepmia* was formally raised to genus level within the Scionini.

9.3 Novel genera of the Scionini

Morphological examination and molecular analysis of the Scionini indicated the presence of two novel genera from Australia and New Zealand. These were formed of a combination of both previously described and novel species, corresponding to *Anzomyia* and *Aotearomyia*.

9.3.1 Genus Anzomyia *Lessard, 2012*

Mackerras (1955) referred to one Australian species, undescribed at the time, as being most similar to *Scaptia* (*Pseudoscione*) based on similarities in the antennal flagellomeres and genitalia, but also sharing the short fleshy proboscis and large, hairy antennal scape, most similar to *Scaptia* (*Pseudomelpia*). It was not until Mackerras' 1960 revision of *Scaptia* that this unnamed species was described as *Scaptia anomala* Mackerras, 1960. Furthermore, Mackerras (1960) identified *Scaptia anomala* as an intermediate species closely related to the former subgenera *Scaptia* (*Scaptia*) and *Scaptia* (*Pseudoscione*), and was provisionally placed within *Scaptia* (*Pseudoscione*) so it would not escape recognition: "*S. anomala* is exceptional, in combining the short proboscis and long palpi

of [the subgenus] *Scaptia* with the diverging frons and general appearance of [the subgenus] *Pseudoscione*... a case could be made for establishing [a new subgenus] for *Scaptia,* [corresponding to] *S. anomala*, and that may prove to be a proper course when more is known about it" (Mackerras 1960, p. 33).

Scaptia anomala was designated as the type species of the novel genus *Anzomyia* (Chapter Four), in addition to the description of three novel species that had accumulated in Australian and New Zealand collections since the work of Mackerras (1955, 1960). Traditional morphological characters were useful in describing these new species, including *Anzomyia chrysomallis* Lessard, 2012 and *Anzomyia pegasus* Lessard, 2012 both from Australia, and *Anzomyia herculensis* Lessard, 2012 from New Zealand. A novel key to species was also developed for the genus to benefit future workers (Chapter Four).

Morphological examination demonstrated the firm separation of *Anzomyia* from the remaining Scionini, distinguished by the diverging frons, proboscis usually short and thick, and subcylindrical palpi with reduced apical pits (Chapters Four and Eight). This was corroborated by the molecular results confirming the large genetic divergence of *Anzomyia* from the remainder of the Scionini, which was recovered as sister to *Aotearomyia* (Chapter Seven; Figure 7.2). Moreover, *Anzomyia* formed a strongly supported and genetically divergent clade represented by multiple specimens of *An. pegasus*. Therefore, *Anzomyia* was accepted as a valid genus of the Scionini based on the morphological and molecular distinctiveness.

9.3.2 Genus Aotearomyia *Lessard, 2014*

In the phylogenetic analysis of the Scionini, the New Zealand species previously belonging to the former subgenus *Scaptia* (*Pseudoscione*) recovered as a well-supported monophyletic clade sister to *Anzomyia* (Chapter Seven; Figure 7.2). This New Zealand clade was also firmly removed from *Copidapha, Parosca* and *Pseudoscione*. Morphology confirmed the distinct separation of the New Zealand clade from the remaining Scionini, distinguished by the stout build, narrow and almost parallel frons that diverges only at the ventral margin, and large slender and tapered palpi with a conspicuous lateral bare area that is often dorsally rotated (Chapters Five and Eight). Therefore, based on the molecular data and distinct morphology, the unique New Zealand clade was described as the novel

genus *Aotearomyia* and the type species *Pangonia adrel* Walker, 1850 was designated, as well as including six previously described species from the former subgenus *Scaptia* (*Pseudoscione*).

9.4 Genera previously belonging to the Scionini

Based on the molecular data (Chapter Seven) and distinct morphology (Chapter Eight), the two peculiar genera *Goniops* and *Caenopangonia* were removed from the Scionini and reassigned to the tribes Goniopsini Lessard, 2014 and Mycteromyiini, respectively. Therefore, the Scionini now comprises 17 distinct genera endemic to the Southern Hemisphere.

9.4.1 Genus Goniops *Aldrich, 1892*

Aldrich (1892) introduced *Goniops* as a monotypic genus from the eastern coast of the United States of America and designated the type species *Pangonia chrysocoma* Osten-Sacken, 1875 (under the synonym *Goniops hippoboscoides* Aldrich, 1982). Mackerras (1955) included this genus in the Scionini, however, molecular results identified that *Goniops* was firmly separated from the Scionini (Chapter Seven; Figure 7.2); *Goniops* recovered as sister to either the Scionini or the Philolichini, depending on the method of phylogenetic inference. Morphological correspondence supported the molecular results, confirming that *Goniops* is strongly divergent from the Scionini and distinguished by the bare eyes, extremely wide frons of the female with a prominent callus, sunken face, cylindrical palpi without a definitive bare lateral concavity or apical pit, and conspicuously reduced proboscis, all uncommon features to the Scionini (Chapter Eight). Therefore, *Goniops* was removed from the Scionini and placed within the novel tribe Goniopsinini Lessard, 2014. This is further supported by the geographical isolation of *Goniops* in the Nearctic, compared to the Scionini that are endemic to the Southern Hemisphere.

9.4.2 Genus Caenopangonia *Kröber, 1930*

Kröber (1930b) originally presented *Caenopangonia* as a genus of the Pangoniinae and designated the type species *Diatomineura hirtipalpis* Bigot, 1892. Mackerras (1955), however, reduced *Caenopangonia* to a synonym of *Mycteromyia* Philippi, 1865. Despite this, Coscarón and Philip (1979, p. 427) resurrected *Caenopangonia* based on the unique morphology and "questionably retained" the genus within the Scionini. Although absent in the molecular analysis, examination of morphology revealed minor differences between *Caenopangonia* and the Mycteromyiini (Chapter Eight). Morphological discrepancies were identified as being vastly greater between *Caenopangonia* and the Scionini, as *Caenopangonia* is distinguished by the presence of the dichoptic eyes in the male, females with extremely wide and densely haired frons with an indistinct subcallus due to the lack of transverse suture, as well as the sunken face, exceptionally strong scutal vittae, and elongated abdomen with rigid cuticle. Furthermore, the genitalia of *Caenopangonia* are more reminiscent of the Pangoniini which were recovered as sister to the Mycteromyiini in the phylogenetic analysis (Chapter Seven; Figure 7.2). Therefore, *Caenopangonia* was removed from the Scionini and reassigned to the more appropriate tribe Mycteromyiini.

9.5 Extended distribution of the Australian Scionini

Several of the recently described species significantly extended the known distribution of the Scionini into unexpected regions of Australia where the tribe was previously thought absent and unable to survive. This was despite some regions having an extensive history of entomological collection. The recently described species *Plinthina arnhemensis* and *Plinthina nelsonae* are the first records of the Scionini from the northern coast of central Australia, including northeast of the Northern Territory and Western Australia, respectively (Chapter Three). Moreover, the recently described species *Myioscaptia lambkinae* extends the known distribution of the Scionini over 700 km NE into central Western Australia where it has not been previously collected (Chapter Six). The most significant extension corresponded to *Copidapha mackerrasi*, collected from Alice Springs in the Northern Territory, and is the only central species of Australian Scionini (Chapter Five). The nearest recorded species to this was over 700 km NE of Alice Springs belonging to *Pl. arnhemensis* collected from Musselbrooke Creek, Lawn Hill National

Park, Queensland. Moreover, *C. mackerrasi* is located over 1200 km NW from the nearest species recorded from within the same subgenus, *Copidapha guttipennis* (Ferguson, 1924), Cleve, South Australia.

These new collection records suggest for the first time that the Scionini appear adapted to tolerate and persist in dry drought prone regions of Australia that are often subjected to extreme temperatures. The Australian genera of the Scionini were previously considered to be limited to mild-temperate to subtropical environments, as the majority of species are restricted to the coastline (Mackerras 1960). Temperature and availability of soil moisture were further thought to restrict the distribution of the tribe, both regulating breeding behaviour, larval development in soil or plant substrate (although little is known regarding the larval biology of the family), frequency of adult emergence, and sustainability of flowers for feeding (Mackerras 1960). Moreover, the recently described species *C. mackerrasi* and *M. lambkinae* are the first records of the Scionini to occur in inland Australia. Both species were collected within close proximity to gorges, presumably surviving desiccation by taking advantage of cooler temperatures during the day and an increase in water availability for larval development. Therefore, additional species of the Scionini are expected to occur in more remote and arid regions of Australia.

9.6 Evolution and biogeography of the Scionini

Divergence time estimation and the fossil record were used to determine whether the current distribution of the Scionini was a result of the sequential fragmentation of the ancient supercontinent of Gondwana (Chapter Seven). Results indicated that the Scionini are a true Gondwanan group and are most likely Australian in origin. Furthermore, a complex process both of vicariance and long distance dispersal appears to have shaped the current biogeography of the tribe.

Mackerras (1960) hypothesised that the Scionini may have evolved in a temperate Antarctica and radiated to New Zealand, Australia and South America. Although the Antarctic taxa are extinct, given the dominant presence of Australian clades with the South American genera nestled within them (Chapter Seven; Figures 7.2 and 7.3), it is plausible that the Scionini are Australian in origin and subsequently radiated outward to the Southern Hemisphere. Based on the molecular results, there appear to be at least three

main waves of radiation from Australia: 1) the colonisation of New Zealand by *Aotearomyia* via long distance dispersal; 2) the radiation of the *Osca* lineage to South America by vicariance; and 3) the radiation of *Lepmia* + *Parosca* + *Scione* + *Pseudoscione* and *Pityocera* + *Fidena* to South America by vicariance. Based on the unsampled taxa, there may be a possibility of two additional radiations of the Scionini from Australia, including a second more recent dispersal to New Zealand by *Anzomyia herculensis* Lessard, 2012, the only New Zealand species of *Anzomyia*, and a separate radiation of the *Pseudomelpia* lineage to South America most likely by vicariance. Mackerras (1960) also suggested that Australian Scionini colonised New Guinea via distance dispersal during the more recent glaciation events of the Pleistocene ice age.

Long distance dispersal of the Australian Scionini to New Zealand may have been facilitated by a series of atolls that once connected Zealandia to the rest of Gondwana, similar to today's Kermadec Islands. Such atolls may have been more pronounced or even connected during periods of glaciation, similar to when mainland Australia was connected to Tasmania during the recent glaciation events 9,000-6,500 years ago. The larvae, some of which are known to develop in close proximity to decaying tree trunks (Coscarón and González 1989), could have floated from Australia to New Zealand and henceforth radiated. While unusual, this hypothesis is plausible given that larval development for the Scionini can take up to three years to complete (Coscarón and González 1989; English 1955), giving individuals time to survive such a journey. Long distance dispersal of Australian species to New Zealand has also been hypothesised for the southeastern Australian bombyliid species *Comptosia moretonii* Macquart, 1855, which is suggested to have been blown across the Tasman Sea to the South Island of New Zealand (Yeates 1991).

An alternative hypothesis for the colonisation of New Zealand may still be explained by vicariance, as the confidence interval of the split between *Anzomyia* + *Aotearomyia* and the remaining Scionini (74.5-32.5 MY; Chapter Seven; Figure 7.3) overlaps with the fragmentation of Zealandia from Gondwana. Mackerras (1957, p. 583) hypothesised that "New Zealand has been too isolated since the Pleistocene for recolonisation to have occurred, but there is enough evidence of recent speciation to suggest rehabilitation of a previously depressed fauna". Either scenario may have led to the colonisation of New Zealand, including vicariance of ancestral fauna that may have suffered an extinction event, such as the drowning of Zealandia during the Oligocene (38-26 MY; Knapp *et al.*

2007), with survivors undergoing recent speciation. Conversely, species might have speciated after the drowning of New Zealand, arriving from Australia more recently via long distance dispersal.

Molecular results indicated that the colonisation of Australia and South America by the Scionini was most likely due to ancient vicariance, perhaps using Antarctica as a biological corridor for migration. Furthermore, the short branch lengths exhibited in the molecular analyses (Chapter Seven; Figures 7.2 and 7.3) suggest that the genera may have undergone rapid radiation, possibly coinciding with the exploitation of new, previously unoccupied niches. These results are somewhat corroborated with the previous molecular work of Cranston *et al.* (2010, 2012) and Krosch *et al.* (2011), who demonstrated that the current Gondwanan biogeographic pattern of the Chironomidae was also formed by complex mechanisms of both vicariance and long distance dispersal.

9.7 Future investigations

Despite the best sampling efforts, several taxa were unable to be included in the molecular analysis and are desired for future molecular studies to confirm their phylogenetic relationships within the Scionini. These include some genera (*Palimmecomyia* and *Pseudomelpia*), subgenera (*Fidena* subgenera *Laphriomyia* Lutz, 1911, *Leptofidena* Kröber, 1930 and *Neopangonia* Lutz, 1909; *Pityocera* subgenera *Pityocera* Giglio-Tos, 1896 and *Pseudelaphella* Kröber, 1930), type species [*Anzomyia anomala* (Mackerras, 1960), *Fidena leucopogon* (Wiedemann, 1928), *Lepmia molesta* (Wiedemann, 1828), *Palimmecomyia walkeri* (Newman, 1857), *Pityocera festae* Giglio-Tos, 1896, *Pseudomelpia horrens* Enderlein, 1925, *Pseudoscione longipennis* (Ricardo, 1902) and *Scione incompleta* (Macquart, 1845)], and morphologically idiosyncratic species [*Copidapha ianthina* (White, 1915), *Copidapha mackerrasi*, *Scaptia aurinotum* Mackerras, 1960, *Scaptia barbara* Mackerras, 1960, *Scaptia limbithorax* (Macquart, 1855) and *Scaptia norrisi* Mackerras, 1960 from Australia; *Anzomyia herculensis* from New Zealand]. More extensive sampling of the New Guinean and South American genera is also desired, in addition to the inclusion of *Caenopangonia*, which is expected to confirm the reassignment of the genus to the Mycteromyiini.

Some of the deeper nodes in the current molecular phylogeny of the Scionini still remain unclear. An integrated approach is recommended to incorporate the revised morphology of the genera of the Scionini in subsequent phylogenetic analyses. Unfortunately, this approach was unable to be used in the present study since there were too few morphological characters available for analysis, especially given that the taxonomic revision and redescription of the genera of the Scionini was directly inferred from the molecular data. Future systematic and biogeographic studies will ultimately benefit from an increased sampling of additional genes and perhaps the inclusion of phylogenomic data.

Further taxonomic revision is still required for the South American genera *Fidena, Pityocera* and *Scione*, given the prominent morphological uniformity of these groups and the outdated diagnostic keys that exclude multiple recently described and synonymised species. Larval and pupal stages are unknown for the majority of the genera of the Scionini and are only rudimentarily described for *Aotearomyia, Copidapha, Myioscaptia, Osca* and *Scaptia*. Although the limited availability of collected material has hindered the development of a thorough diagnosis for these stages, the immatures may provide a suite of putatively useful and informative characters for future phylogenetic studies of this fascinating and ecologically important group of Diptera.

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